Status, Impact, and Recommendations for Research and Management

of Exotic Invasive Ants in Christmas Island National Park

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Executive Summary

1. *The exotic invasive ant,* Anoplolepis gracilipes*, accidentally introduced to Christmas Island sometime between 1915 and 1934, is now spreading through the undisturbed rain forest on the island.*

   - Our limited surveys identified at least six separate infestations, ranging in area from several hectares to at least one square kilometer.

   - As of December 1998, the total known areal extent of infestation approximated 2-2.5 km^2, comprising about 2-3 percent of all intact rain forest on the island, but a much larger fraction of shore terrace forests.

   - Spread can be rapid. Some "hotspots" of infestation can increase ten-fold in area over a year. Infestations may spread at three meters per day.

2. *In areas of infestation,* A. gracilipes *forms extensive, multi-queened "supercolonies."*

   - *Anoplolepis* is a generalist consumer – a scavenger, a predator on both invertebrates and vertebrates, and it depends heavily upon honeydew produced by plant-feeding scale insects.

   - In areas of supercolony formation, high densities of foraging workers are sustained on the forest floor and across almost all plant surfaces, including canopy trees. Activity of foragers is continuous.

   - *Anoplolepis* colonies are thought to spread through "budding" where queens and associated workers move on foot to establish in new areas.

3. *Invasion by this exotic ant destroys ecosystem integrity of rain forest on Christmas Island. Consequences include:*

   - Impacts from elimination of the red land crab from ant-invaded areas. In areas of supercolony formation, *Anoplolepis* kills and eliminates the dominant red land crab. The deaths of millions of red land crabs in ant-invaded areas has removed the regulatory controls these crabs impose on seedling recruitment and litter breakdown. As a consequence, the forest ecosystem (habitat structure, plant species composition, and ecosystem processes) is rapidly transformed in *Anoplolepis*-invaded areas.

   - Impacts arising from the association of crazy ants with scale insects. Supercolony formation of crazy ants is associated with population outbreaks of plant-feeding scale insects. In turn, these scale outbreaks are associated with canopy dieback, especially of one of the dominant canopy tree species, the Tahitian chestnut (*Inocarpus fagifer*).

   - Impacts of crazy ants on species of conservation value. *Anoplolepis gracilipes* presents a direct, broad threat to many notable island species, including listed vulnerable and endangered species. Because this exotic ant sustains high densities and has broad foraging and nesting habits, it threatens species which nest or live in the forest canopy (e.g., Abbott's booby, CI frigate bird, CI gecko), subcanopy (e.g., CI Hawk-Owl), understorey (e.g., CI Thrush), or on the forest floor (e.g., CI shrew, robber crab, CI blue-tailed skink). If supercolonies of *Anoplolepis* continue to form and spread across the island, marked reduction and even extirpation of some species is possible.

Recommendations for action

1. *Establish the spatial scale and tempo of ant invasion.*

   - Systematically survey the distribution and abundance of *Anoplolepis gracilipes* across the island. Survey is required outside park jurisdiction since *Anoplolepis* does not respect park boundaries. Repeated surveys are necessary to determine the island-wide dynamics of spread.

   - Design surveys so that they can be integrated into and build upon the existing Christmas Island Geographic Information System.

2. *Assess the impact of* Anoplolepis *on conservation values. Three foci are recommended.*

   - Analyze the population dynamics of *Anoplolepis*, its interactions with scale insects, and their role in understorey and canopy dieback. These studies will determine the temporal stability of invasive ant and scale insect populations, rate and means of spread, and help evaluate designs for control and containment efforts.

   - Assess the impact of *Anoplolepis* on the dominant red land crab, follow the cascading effects caused by crab removal, and develop a monitoring program for long-term effects on ecosystem integrity. Such studies will identify the nature, rate, and scale of ecosystem change, information necessary to determine the magnitude of control/containment efforts.

   - Assess the impact of this invasive ant on island species of concern, including selected endemic seabirds, land birds, bats, and reptiles. These results will inform on the likely impact of invasive ants on Christmas Island endemic fauna and species listed under the Endangered Species Protection Act.

3. *Initiate a control/containment program in three steps.*

   - Begin immediately to develop criteria, protocols, and costs for effective toxic baiting against *Anoplolepis*, including monitoring of target and non-target impacts.

   - Develop strategies to contain existing infestations of *Anoplolepis*. Efforts should focus on population depletion and containment rather than eradication of infestations.

   - Establish criteria for Special Ecological Areas (SEA) in uninvaded areas of island rain forest. Establish an expert panel to develop SEA criteria and nominate SEAs.

   - Use established protocols to prevent spread of ants into selected trial SEAs.

4. *Consider* Anoplolepis *invasion in the broader management plans for Christmas Island National Park.*

   - Revisit approved, pending, and draft Recovery Plans for threatened species under the Endangered Species Protection Act in light of potential impacts of the crazy ant.

   - Incorporate impact assessment and mitigation in any revision of the Christmas Island National Park Plan of Management.

   - Provide information to residents and workers on Christmas Island to minimize unintended transport of *Anoplolepis* from infested to uninfested areas. Use the *Anoplolepis* invasion to illustrate the advantages of prevention of entry, through a strict, effective quarantine service, as the best strategy to prevent future pest problems on the island.

Introduction

Social insects, primarily ants, termites, and wasps, are among the most potent of invaders, both on continents and islands. Their rates of introduction have greatly accelerated over the last century, primarily through increasing human commerce. Some ant species, known widely as "tramp" ants (Wilson and Taylor 1967), share features that make them especially effective invaders. These interlinked features include high reproductive rates, broad niche, polygyny (many queens), colony budding, and lack of intraspecific aggression (Moller 1996, Holway *et al.* 1998). For example, polygynous colonies of the invasive Argentine ant (*Linepithema humile*) in California show little intraspecific aggression, even over large spatial scales (> 100 km) and colonies without intraspecific aggression have higher reproductive rates and larger populations of workers. And, once population levels of these ants build up, their effects can be devastating. In Hawaii, the Argentine ant displaces soil and litter arthropods and interferes with native pollinators (Cole *et al.* 1993). The polygynous form of the red imported fire ant (*Solenopsis invicta*), originally from South America, has spread rapidly across the southeastern United States, displacing resident ants, decimating soil and litter arthropods, killing juvenile birds and mammals, and causing health risks for farm workers (Porter and Savignano 1993, Vinson 1994).

Effects of these ants are felt especially on oceanic islands, which lack well-developed ant faunas. Oceanic islands are usually viewed as more susceptible to alien invaders than continental areas. Reasons proffered for susceptibility to invaders are intuitively appealing but not without controversy (Simberloff 1989, Lake and O'Dowd 1991). Nevertheless, because island biota have evolved in relative isolation and in the absence of many forces shaping continental organisms, ecosystems of ocean islands may be particularly susceptible to invasion by some alien species from continents. Most oceanic island ecosystems appear

exceptionally vulnerable to damages caused by alien plants and animals (Loope and Mueller-Dombois 1989, D'Antonio and Dudley 1995).

This report describes the results of our research on the invasive exotic ant *Anoplolepis gracilipes* (Fr. Smith)(Hymenoptera: Formicidae) on Christmas Island, Indian Ocean from 21 November - 13 December 1998. Here we describe the natural history of *Anoplolepis* and what is known about its short history on Christmas Island. We then report on our surveys of the distribution of *Anoplolepis* infestations on the island, assess aspects of its impacts on the integrity and conservation value of the rain forest ecosystem, and forecast possible impacts on species of conservation value. Finally, we make several recommendations for research and management to mitigate the impact of this invasive ant.

Anoplolepis gracilipes as a "tramp" ant

Anoplolepis gracilipes is an important 'tramp' ant species (Table 1, Plate 1). Possibly of West African origin (Wilson and Taylor 1967), it is now widely distributed in the tropics, especially in East Africa, Asia, and the Pacific. *Anoplolepis gracilipes* is a well-known crop pest because it protects scale insects that damage tropical perennial crops, such as coffee and cacao (Van der Groot 1916, Nixon 1951, Haines and Haines 1978a, Way and Khoo 1992). It is commonly called the "crazy ant" because of its rapid movements and frequent changes of direction, especially when disturbed (Haines *et al.* 1994). Because *A. gracilipes* is highly predatory, researchers have explored its use as a potential biological control agent in control of insect pests of crops such as coconuts and cocoa (Brown 1959, Greenslade 1972). This generalist consumer has even been actively introduced into plantations in efforts to control plant pests (Room 1973). However, the damage caused by the scale insects that typically accompany *Anoplolepis* outweighed any benefits from reduction of the target pest, and these efforts were sidelined.

Anoplolepis gracilipes has accompanied human commerce and spread widely across oceanic islands, both in the Indian and Pacific Oceans. As such, Wilson and Taylor (1967) classified it among the "tramp" ant species – those with a suite of characteristics that make them particularly effective invaders of islands (see above). Aside from continental areas and islands, including India, Sri Lanka, South Africa, Indonesia, Myanmar, Malaysia, and New Guinea, it has established on Indian Ocean islands including the Seychelles, Mauritius, Reunion, and the Cocos Islands. In the Pacific, it is known from the Hawaiian Islands, French Polynesia, Okinawa, Vanuatu, and Micronesia. In many instances, the crazy ant is a pest in households and in public buildings (Lewis *et al.* 1976, Haines and Haines 1978a, Veeresh and Gubbaiah 1984). Two reports indicate that they may represent a nuisance to humans. In the Seychelles, Haines and Haines (1978a) reported that *A. gracilipes* irritated some people, especially when "attempts to brush them off caused the release of formic acid, which increased the irritation and often attracted more ants." Veeresh and Gubbaiah (1984) described that crazy ants… "caused burning irritation to the eyes, whenever hands contacted with ants touched the eyes."

Crazy ants have a broad diet. Like all ants, they require proteinaceous foods for brood production. In the Seychelles, they are known to feed on invertebrates, and, in culture, attack, kill, and dismember large arthropods (Haines *et al.* 1994). In the field, they capture ants of other species as well as a wide range of other insects, isopods, myriapods, molluscs, and arachnids. In Hawaii, where *Anoplolepis* was introduced in the 1950s, *Anoplolepis* is associated with decreased occurrence and density of endemic spiders at elevations up to 1000 m (Gillespie and Reimer 1993). Further, it is implicated in the depletion of the native arthropod fauna in riparian habitats in the lowland forests (Hardy 1979). Occasionally, *Anoplolepis* has even been observed carrying small reptiles and other vertebrates (Haines *et al.* 1994). Surveys of the pest status of *Anoplolepis gracilipes* in the Seychelles reported that

they crawled over and irritated dogs, pigs, and rats; killed newborn pigs, dogs, cats, rabbits, and rats; irritated chickens when brooding, often forcing them to move away; killed new chicks when moist from the egg; and, killed snakes and lizards (Haines and Haines 1978a).

The crazy ant is highly dependent on honeydew produced by scale insects and precipitates population outbreaks of scale (Van der Groot 1916, Nixon 1951, Haines and Haines 1978a). In Java, the scale insect *Coccus viridis* flourished in the presence of crazy ants, with an average of 1,057 scales per coffee bush, compared to 70 on ant-free bushes (Van der Groot 1916). Further, parasitization of scale by hymenopterous enemies was much greater on ant-free bushes (39%) than on those protected by *Anoplolepis gracilipes* (6%). Similarly, de Fluiter (1939) described that the severity of infestations of the scale insect *Pseudococcus citri* in coffee plantations in Java was positively related to the abundance of *Anoplolepis gracilipes*. In plantations where this ant was absent, scale outbreaks were only sporadic. Both Van der Groot (1916) and Betrem (1936) have reported that *Anoplolepis gracilipes* moves scale crawlers to new host plants where it establishes new populations of scale insects.

Scale insects, through their feeding activities and possibly disease transmission, can be debilitating to their host plants (Vranjic 1997). Foraging *Anoplolepis* descending trees after tending scale often have greatly distended, almost translucent gasters, indicative of honeydew feeding (Haines and Haines 1978a). In the Seychelles, the quantity of honeydew has been estimated to constitute 50% of the body weight of a 2.5 mg worker (Haines *et al.* 1994). Further, in areas where *A. gracilipes* occurred more than 90% of all trees and shrubs showed signs of sooty mould, affecting citrus and cinnamon crops (Haines and Haines 1978a).

In the field, *A. gracilipes* forages throughout the day and night, and over a wide range of temperatures (Greenslade 1972, Haines and Haines 1978b). Foraging continues

throughout the year, and there is a continuous, but fluctuating, production of worker larvae, pupae, and eggs (Baker 1976). In some cases, sexuals can also found throughout the year (Haines and Haines 1978b), but in others their production is highly seasonal and occurs just prior to the rainy season (Baker 1976). Both males and queens are winged but mating flights have never been observed (Rao *et al.* 1991, Haines *et al.* 1994). Dispersal occurs through colony budding; winged and unwinged queens can be seen walking in the open, accompanied by workers (Lewis *et al.* 1976, Rao *et al.* 1991, D.J. O'Dowd, pers. obs.).

Nesting requirements for *Anoplolepis gracilipes* are generalized; they nest under leaf litter, in cracks and crevices (Lewis *et al.* 1976, Rao and Veeresh 1991). In Papua New Guinea, *Anoplolepis gracilipes* typically nests under leaf litter or in holes in the ground, but forages over every surface within its territories, including forests trees (Room 1975). In coconut plantations, *A. gracilipes* nests in the crowns of coconut palms and feeds on nectar secreted from male flowers and from honeydew-producing scale insects (Young 1996).

Known history of the introduction and invasion on Christmas Island

The crazy ant was not reported in the initial monograph produced by C. Andrews (Andrews 1900) or in subsequent publications on the island's invertebrates up to 1915. Although, W.C. Crawley collected four ant species from Christmas Island in 1915 (Crawley 1919), *A. gracilipes* was not described from the island until 1934 (Donisthorpe 1935). We contacted D.A. Powell, probably the person most knowledgeable about the natural history of Christmas Island through the 1960s-1970s, the period of most rapid expansion of road construction and mining on the island. In a letter he reported that he was familiar with the ant but never saw infestations. Campbell (1964), in a survey of insects of medicinal, veterinary, agricultural, and forestry concern did not list *Anoplolepis*, despite reporting on the occurrence of scale insects and three other ant species. He did report the occurrence of

Tachardina aurantiaca, the major scale associated with *Anoplolepis* on the island, but gave no indication of its abundance or distribution.

J. Tranter and P.T. Green made the first reliable report of which we are aware of supercolony formation by *Anoplolepis* in 1989. They observed high densities of crazy ants (identified by R.W. Taylor) associated with many dead read crabs in forest below Taman Sweetland near the rock crushing plant. Subsequent to that observation, in 1995 Roger Hart reported the occurrence of high densities of an ant consistent with the behaviour of *Anoplolepis* between Northwest Point and West White Beach. In the course of monitoring our long-term exclusion experiments of red land crabs, we first noted and confirmed *Anoplolepis* supercolony formation along the shore terrace near Tait Point in late November 1997. Subsequently, we examined supercolonies in shore terrace above Greta Beach and along the Dales-Martin Point Track in December 1997. At that time we set up 10 4 m x 4 m plots in invaded and adjacent uninvaded areas at each of those two locations to compare ant activity, crab burrow densities, and seedling abundance and diversity. We informed both the Natural Resources Manager and the Conservator on the island of our preliminary findings. We were sufficiently concerned that we wrote a letter to Parks Australia North detailing our findings. Subsequently, we initiated the studies on which this report is based.

Survey for *Anoplolepis* supercolony formation

<u>Procedures</u>. We defined supercolonies as areas with a continuous distribution of *Anoplolepis* workers at extremely high densities, so much so that when disturbed the ants "boiled" up off the soil/litter surface and swarmed over field workers. Supercolony formation can occur among polygyne (i.e., multi-queened) colonies of some ant species, including invasive red imported fire ants (*Solenopsis invicta* - Porter *et al.* 1988), argentine ants (*Linepithema humile* - Holway *et al.* 1998), and crazy ants (*Anopolepis gracilipes* -

Lewis *et al.* 1976). In this case, the distribution of nest sites is diffuse and single colonies cannot be defined.

Infestations were defined in two ways, assuming a temporal sequence in invasion. Recent (< 1 year) invasions were defined as those areas where supercolonies of *Anoplolepis* had recently formed. These sites were characterized by the presence of crab burrows being actively invaded and used as nest sites by *Anoplolepis*, dead red crabs that were usually still intact, few small (or no) seedlings, and intermittent litter cover. Older, established invasions (> 1 year) were generally characterized by the absence of crab burrows, fragmented bleached crab exoskeletons as well as "fresh" dead red crabs, abundant larger seedlings, and deep litter cover. *Anoplolepis* generally nested in decomposing woody debris at these sites.

The distribution of *Anoplolepis gracilipes* supercolonies was surveyed using the existing network of roads and tracks, and by foot along drill lines and the shore terrace. Because we had limited time (further reduced by 5 days due to the strike of the Christmas Island Workers Union) and personnel, our survey was not systematic. Instead, we used our knowledge of known infestations and reports gathered from island residents to help direct our efforts. The actual distribution of the ant across the island is much wider than these areas of supercolony formation, but has not been determined. For example, we have found foraging workers of *Anoplolepis* in Settlement and at the Education and Research Centre without any evidence of supercolony formation.

Areas surveyed included: (1) The Dales-Martin Point Track, (2) Shore terrace from Northwest Point back to Martin Point, (3) Shore terrace from Northwest Point to West White Beach, (4) West White Beach Track, (5) Upper terrace slopes north of the Central Area Workshop, (6) The Blowholes Track west to the base of the old Blowholes Track, (7) The Boulder Track south from the Blowholes to South Point, (8) Powerline Track to South Point, (9) Circuit Track (to 3 km in from gate along Winifred Beach Track), (10) Greta Beach

Track, (11) Dolly Beach Track, (12) Margaret Knoll Track, (13) Waddell Hill (northslope), (14) Stronarch Hill (to terrace slopes, perpendicular to North-South Baseline Road), (15) Lily Beach Road, (16) Ethel Beach Track, (17) upper terrace forests below Field 17, (18) Winifred Beach Track above the carpark, (19) Shore terrace behind the Chinese cemetery in Settlement, (20) Shore terrace at the southern end of the golf course, (21) Area below the rock crushing plant, (22) Terrace forest near the old Chinese Cemetery below the golf course lookout, and (23) Forest adjacent to Field 22S, near the Circuit Track. In areas of supercolony formation, we estimated the location and extent of infestation along the track or road, either using an automobile odometer or by counting out paces from a reference point.

Results and observations. We found supercolony formation of *Anoplolepis gracilipes* in at least six locations, including areas inside and outside the boundaries of the National Park (Figure 1A). Most areas of supercolony formation were found along the shore terrace, although some infestations occurred in plateau (forest adjacent to Field 22S) and higher terrace areas (e.g., below Stronarch Hill and in Hidden Valley)(Table 2). Established infestations were widespread on the island, occurring in all quadrants of the island, including the shore terraces from the Blowholes to South Point, terrace forest above the Winifred Beach Car Park, shore terraces above Dolly Beach and Greta Beach, plateau forest in Hidden Valley, and the shore terrace from The Dales to Martin Point through to Northwest Point and on to West White Beach. Recent invasions were found in three locations: our Murray Hill study site, plateau rain forest adjacent to Field 22S, and on the plateau "shoulder" (upper terrace slope) east of Stronarch Hill. In these areas, crazy ants were establishing nests in crab burrows, seedling densities were low, seedling sizes were small, and litter cover was not markedly high. We were unable to relocate the infestation reported in 1989 below Taman Sweetland by J. Tranter and P.T. Green. Supercolony formation has been reported at Hosnie Springs, Smith Point, near the Drumsite water tank (J. Haydock, pers. comm.), and on the

western slopes of Waddell Hill (R. Paine, pers. comm.) although we have not verified these observations.

We estimated that the total area of supercolony formation was approximately 200-250 hectares (2 – 2.5 km^2)(Table 2) in December 1998. The largest and most extensive invaded area surveyed was the shore terrace ranging from The Dales to Martin Point through to Northwest Point and on to West White Beach where approximately 100-150 ha had been invaded. These estimates, both island-wide and within specific areas, are likely to be conservative since we were unable to systematically survey the island. Further, it is unclear whether some of the "adjacent" infestations are actually linked and continuous. The infestation along the South Point Powerline Track is likely to link with the first, northerly infestation running along the shore terrace below it at Tait Point (Figure 1A). Similarly, it is possible that the infestation near Stronarch Hill is contiguous with that above Greta Beach, and that the infestation at the high terraces at Hidden Valley form a continuous supercolony with that along the Dolly Beach Track. If so, our estimate of the areal extent of invasion would be much higher. Of similar concern is our lack of information on the status of the shore terrace from West White Beach below our Murray Hill study site and through to the invaded area below the Central Area Workshop.

Little is known about the rate of spread of *Anoplolepis* supercolonies on Christmas Island. We have some information about the infestation size at Tait Point in December 1997 and again in December 1998. In 1997, we paced off approximately 100 m of infested shore terrace, approximately one hectare, along the Boulder Track. By 1998, this had expanded southward an additional 1100 meters. Interestingly, the northern boundary of the infestation has remained static. This represents a greater than ten-fold increase in area over one year. Assuming that crazy ants spread through colony budding from the southern boundary, this represents an average spread of about three meters per day, even more rapid that the one

meter per day spread reported on Mahé in the Seychelles (Haines and Haines 1978a).

Similarly, the infestation along the Dales-Martin Point Track was much more extensive in

1998 than in 1997.

Clearly, more extensive, systematic survey is a critical need in assessing the status of

the invasion and island-wide rate of spread. Our initial observations in December 1997,

made in shore terraces with high light levels and uneven canopy cover, made us think that

supercolony formation could be restricted to these coastal forests. Given that we have now

found supercolonies in Plateau Forest adjacent to Field 22S, in Hidden Valley, and at our

long-term study sites at Murray Hill, we can find no obvious reason that *Anoplolepis* will not

continue to invade plateau forest and extend its distribution beyond the terraces.

Impact of *Anoplolepis* on forest structure and processes

Land crabs, especially the red crab (*Gecarcoidea natalis*), are dominant consumers

on the forest floor across Christmas Island and are a key determinant of forest structure and

processes (O'Dowd and Lake 1989, 1990 1991, Green 1997a,b, Green *et al.* 1997, in press).

We have had crab exclusion experiments in train near Murray Hill and southwest of the

Blowholes for nine and four years, respectively (Figure 1B). These experimental

manipulations of red crab densities showed that removal of red crabs from forest plots

precipitated dramatic and persistent changes in rates of litter breakdown, abundance of litter

mesofauna, and seedling density and diversity both in light gaps and the shaded understorey

(Green *et al.* 1997a,b, Green *et al.*, in press). Most of these effects are mediated directly by

red crabs, since they include litter, and seeds and seedlings of many species in their diet.

Thus, in intact rain forest, the red crab is a central element in the rain forest interaction web.

Procedures. We assessed experimentally the direct impact of *Anoplolepis* on red land

crabs along The Dales-Martin Point Track by determining the fate of caged crabs in an area

of *Anoplolepis* supercolony formation and in an uninvaded, control site. Fourteen red crabs

(average carapace width was 8.2 cm) were collected and placed in wet leaf litter overnight. The following morning, seven crabs were confined individually in wire mesh cages (1.5 cm x 2.0-cm openings) in the ant-invaded area and seven in the control area. Cages were fixed in place with metal pegs, and covered with leaf litter. The condition of caged crabs was inspected after 24 h. We further explored whether ant use of burrows was related to the absence of live crabs from burrows. In December 1997 at the invaded site along The Dales-Martin Point Track, we excavated 28 burrows in which *Anoplolepis* was nesting and 21 burrows without ant nests and determined whether live crabs were present.

To assess impacts of the crazy ant on land crabs and how their deletion from the interaction web affects some aspects of forest structure and processes, we used comparisons of sites invaded by *Anoplolepis* paired with uninvaded, control sites in each of six areas (Figure 1B). Within approximately two hectares at each invaded site, we set out haphazardly five 4 m x 4 m permanent plots. We then located the nearest uninvaded, intact forest of similar structure and set out five 4 m x 4 m plots in the same manner. In total, we sampled 80 m^2 each in invaded and control plots in each of six areas (60 plots, a total of 960 m^2). We used the same invaded and control sites along The Dales-Martin Point Track and above Greta Beach as we did in December 1997.

On each plot, we first assessed ant activity at sugar baits: one 5 cm x 5 cm Wettex™ pad soaked in a 30% v/v sucrose solution was placed haphazardly in each plot. After 20 minutes, each pad (and any ants feeding on the pad) was collected and placed in 50% ethanol. Ants were then counted and vouchers of each species at each site collected for later identification. We then counted the numbers of dead land crabs (red crabs, robber crabs, and blue crabs) lying on the forest floor and crab burrows (intact burrows and those occupied by *Anoplolepis*) in the same plots. The ant activity index was calculated as the total number of

ants recovered from the sugar bait within a plot, divided by the number of minutes the bait was exposed.

If crab numbers were reduced in areas of *Anoplolepis* invasion, we expected differences in litter cover and seedling recruitment between invaded sites and their paired control sites. Standing litter cover on each plot was estimated with the point-quadrat method. A 6 x 6-point 0.25 m^2 litter frame was placed haphazardly in each plot and the number of points covered by litter tallied. Numbers, sizes (height in mm), and species identity of seedlings on each plot were determined. Species diversity was calculated using Simpson's Index of Diversity. For analysis of results, blocks (paired sites, n = 6) were used as replicates. Data for each variables were pooled for the five invaded plots and five control plots within "treatments" (invaded, control) in each block and analyzed using a randomised-block ANOVA (SYSTAT 7.0). Residuals were inspected and data transformed as necessary to improve homogeneity of variances. We used Numerical Multidimensional Scaling (using the Bray-Curtis similarity coefficient) and ANOSIM (analysis of similarities) on log (x+1)-transformed data to compare relative species abundance of seedlings on invaded and uninvaded, control sites (PRIMER™; Clarke and Warwick 1994). ANOSIM is a non-parametric permutation procedure which tests hypotheses about sample (site) similarity.

Results and observations. In invaded areas, densities of foraging *Anoplolepis* in the litter were extraordinary, often well above 1000 ants m^{-2}. The smallest of disturbances sent waves of alarm response through local patches of this ant so much so that they then swarmed rapidly over our pant legs and sometimes onto our torsos. These worker ants foraged on almost all available surfaces, including the soil and litter on the forest floor, seedlings and saplings, understorey shrubs and vines, subcanopy trees, and up and down the boles of canopy trees. Ants foraging on vegetation usually tended scale insects, particularly the lac insect, *Tachardina* ?*aurantiaca* (Plate 2A) and several unidentified species of soft scale

insects. We usually found it impossible to identify discrete nests of *Anoplolepis*. Nest sites were extremely generalized, often occurring under litter, below stones, at the bases of trees, in decomposing woody debris on the forest floor, in burrows of red crabs, in treeholes on a variety of trees (*Inocarpus*, *Celtis*, *Syzgium*, *Barringtonia*) and in the leaf axils of the *Arenga* palm, a common tree species across the island. Indeed in some areas, kicking litter or disturbing crab burrows would induce crazy ants to gather up brood and carry them about. Densities of ants foraging in control, uninvaded areas was much lower, usually <10 ants m^{-2}.

Ant activity at sugar baits was three-fold higher in areas invaded by *Anoplolepis* (Figure 3A, Table 3A, Plate 2B) than in uninvaded, control areas. This significant difference was attributable entirely to the activity of *Anoplolepis*. Indeed, the activity of other ants on sugar baits was reduced significantly in invaded areas relative to control areas without *Anoplolepis* (Figure 3A, Table 3A). Our impression is that ant species diversity at sugar baits was reduced in areas invaded by *Anoplolepis*, but formal comparison of ant species richness between invaded and control areas awaits authoritative identification of the ant voucher specimens. Some ant species found on sugar baits in uninvaded, control areas were never seen at baits in areas invaded by *Anoplolepis*. These included *Paratrechina* sp. A and *Odontomachus simillimus*, *Solenopsis geminata*, *Pheidole megacephala*, and *Monomorium* spp. One species, however, the bigheaded ant (*Pheidole megacephala*), commonly co-occurred on sugar baits with *Anoplolepis*.

Anoplolepis foragers killed red crabs confined in mesh cages. Over 24 h, four of seven red crabs placed within the *Anoplolepis* supercolony along The Dales-Martin Point Track were dead after 24 h exposure. In the control area, all red crabs survived. In fact, five of seven forced their way out of the cages and escaped. Exactly how ants kill red crabs is unclear. *Anoplolepis* swarmed over the red crabs which "twitched" frequently. After 24 h, all crabs had lost their bright red colour and faded to pale orange. Of the three surviving

crabs, one was reasonably active but the other two were very sluggish. The two sluggish crabs had autotomized walking limbs. Further, all four dead crabs had also autotomized limbs. All crabs had discoloured, blackened mouthparts and the internal surface of the abdomen of dead crabs was wet. Brown fluid was found on leaf litter below these crabs. These observations are consistent with those we made on free-ranging red crabs in *Anoplolepis* infestations along The Dales-Martin Point Track, Dolly Beach Track, above Greta Beach, in Hidden Valley, and along the Winifred Beach Track. In all instances, red crabs were lethargic and did not show typical movement patterns or range of behaviours (e.g., alarm response to human presence). On closer inspection, almost all crabs had blackened mouthparts and some were "bubbling" at the mouth. We also observed *Anoplolepis* swarming on berried females migrating seaward along The Dales-Martin Point Track. *Anoplolepis* actively attacked the exposed egg masses of these females (Plate 2C).

When red crab burrows were present in invaded sites, *Anoplolepis* routinely used them as nest sites. At The Dales-Martin Point infestation, the presence of live red crabs in their burrows depended on the absence of *Anoplolepis* ($\chi^2 = 25.56$, P < 0.001, chi-square test). Live red crabs were never found in ant-occupied burrows (0/28), and in the absence of *Anoplolepis*, 72% (15/21) of sampled burrows were occupied by live red crabs (Figure 4). When we disturbed burrow entrances with twigs, ants usually poured out, sometimes carrying brood. When these burrows were excavated, brood (eggs, larvae at various stages of development, pupae) were usually present, and sometimes winged males.

Land crab deaths on the forest floor were massive in 5 of 6 invaded sites and occurred in all invaded areas sampled (Figure 3B, Table 3B, and Plate 2D). Only two dead crabs were found in uninvaded, control sites, both in plots above Greta Beach. By far the majority of dead crabs on the forest floor were red crabs, although at some sites we found dead robber crabs (The Dales-Martin Point Track, Dolly Beach Track, Winifred Beach

Track) and blue crabs (The Dales-Martin Point Track, Dolly Beach Track). In invaded areas, we counted an average of about one dead red crab for every two m^2 of forest floor we inspected. Because we sampled immediately after the migration period of the red crab, crab mortality was sometimes extraordinary. For example, in some patches of the invaded site above Winifred Beach, dead red crabs exceeded six per m^2. Nevertheless, we occasionally encountered some live crabs, mainly distressed red crabs, but also a few robber crabs, in invaded areas. *Anoplolepis* workers were usually swarming on these individuals.

Very few intact crab burrows were found in ant-invaded areas and burrow densities of red crabs showed an inverse pattern to crab mortality (Figure 3C, Table 3B). Pooled over all invaded sites, only 15 burrows were found and *Anoplolepis* occupied 11 of these. At uninvaded, control sites, intact burrows averaged over one per m^2, and were typical of densities seen elsewhere on shore terraces.

Standing litter cover differed strongly between *Anoplolepis*-invaded and uninvaded, control sites (Figure 4D; Table 3C), and in the absence of red crabs accumulated to high levels (Plate 2E, F). Litter cover in invaded sites (87%) was double that measured in control sites (43%). Because these measurements were made at the end of the dry season over which red crab activity is lower and leaf litterfall is higher than in the wet season (Green 1997, Green 1998), they probably represent the minimum cover differences between invaded and control areas. These results are consistent with those seen in our long-term crab removal experiment near Murray Hill (Green *et al.*, in press).

All uninvaded, control areas showed the typical, but unique structural feature of rain forest on Christmas Island – a remarkably open understorey (Plate 2G, Hicks *et al.* 1984). However, the understorey of *Anoplolepis*-invaded forest differed radically, and a diversity of seedlings usually carpeted the forest floor (Plate 2H). Overall, seedling densities were over 30 times greater in *Anoplolepis*-invaded sites than in uninvaded, control sites (8255 seedlings

vs. 268 seedlings, respectively). In *Anoplolepis*-invaded areas, seedling densities averaged 1375 seedlings/80 m^2 whereas in uninvaded areas, mean seedling densities were just 45 seedlings/80 m^2 (Figure 4A, Table 3D). Species diversity of seedlings, measured as the total number of seedlings per site and as Simpson's index of diversity, was also significantly higher at *Anoplolepis*-invaded sites (Figure 4B,C, Table 3F,G). Average species richness of seedlings was over four times greater at invaded sites than at the uninvaded, control sites (22 vs. 6 species/80 m^2, respectively).

The NMDS/Analysis of Similarities (ANOSIM) analyses showed marked differences in the relative species abundances of seedlings between invaded and uninvaded areas (Figure 5). The ant-invaded and control sites separated distinctly and significantly in the ordination (ANOSIM, $p < 0.009$). The relative species abundance in the invaded area at Tait Point showed the greatest difference to other *Anoplolepis*-invaded areas, as reflected in the significant interaction term between 'block' and 'invasion' in the ANOVA for Simpson's diversity index (Table 4D). Species diversity at this site, with a strong dominance by *Barringtonia racemosa*, was lower than at other sites.

Species composition of seedlings differed markedly between invaded and uninvaded sites (Figure 6). Of a total of 17 species were recorded overall in uninvaded, control sites, seedlings of *Barringtonia racemosa* (30%), *Inocarpus fagifer* (25%), and *Tristiropsis acutangula* (24%) were dominant and comprised most seedlings recorded (211 of 268 seedlings). In invaded sites, a diversity of seedling species was present. Overall, of the 33 species recorded, seedlings of *Arenga listeri* (18%), *Celtis timorensis* (14%), and *Pisonia umbellifera* (12%) were most abundant, but none were overwhelmingly dominant.

These patterns in seedling density and diversity are remarkably consistent with those on our crab removal experiments at Murray Hill and the Blowholes. Eliminating crabs, either by experimental removal (Green *et al.* 1997a, b) or by the invasive ant *Anoplolepis*

gracilipes, released seedling recruitment of those species with seeds or seedlings susceptible to red crab predation (e.g., *Pisonia umbellifera*, *Planchonella nitida*, *Syzgium nervosum*). In uninvaded, control areas, red crabs maintained a sparse seedling community composed mostly of the relatively resistant *Barringtonia*, *Inocarpus,* and *Tristiropsis*.

We have some initial information on the temporal stability of *Anoplolepis* invasion and impact, because we monitored impacts in two areas, along The Dales-Martin Point Track and above Greta Beach, in both December 1997 and 1998. We will only summarize these results here.

(1) Ant activity indices and activity of *Anoplolepis* were consistent at invaded sites over the two years, and we noted no obvious changes in ant densities or activity at either site.

(2) Crab mortality on the forest floor in invaded areas was high, but variable, in both years. At The Dales in 1997, an average of 10 dead crabs were found on each plot and in 1998, just over 3 dead crabs per plot. At Greta in 1997, an average of 6 dead crabs was found on each plot and in 1998, 22 dead crabs were found on each plot.

(3) Burrow densities on invaded plots did change between years at both sites, suggesting that invasions at both sites had initiated sometime in 1996-1997. In December 1997, burrow numbers were high at both sites (The Dales, a mean of 10.9 burrows per 16 m^2 plot; Greta, 16.7 burrows per plot), but large fractions of these had been occupied by *Anoplolepis* and used as nest sites (75% at The Dales, 63% at Greta). By December 1998, burrow numbers had plummeted: we tallied an average of two burrows per plot at The Dales, and *Anoplolepis* occupied all of these. At Greta, plots averaged less than one burrow; *Anoplolepis* occupied 1 of these 4 burrows.

(4) In both 1997 and 1998, seedling densities and diversity were high on invaded plots. At The Dales, an average of 155 and 212 seedlings occurred on each 16-m^2 plot in 1997 and 1998, respectively. Species richness of seedlings was similar in both years, 9.2

species per plot in 1997 and 5.4 in 1998. At Greta, an average of 159 and 194 seedlings occurred on each 16-m^2 plot in 1997 and 1998, respectively. Species richness of seedlings was also similar between years (12.8 species per plot in 1997 and 9.6 species per plot in 1998. Control levels were uniformly low in 1997; however, in 1998, *Anoplolepis* had invaded the control site. Seedling densities on these plots were intermediate, averaging 31.4 seedlings per 16-m^2 plot, but species richness, averaging 9.2 species per plot, was comparable to other invaded sites.

These results indicate that high densities of *Anoplolepis* can be sustained for at least one year, that this ant appears to eliminate red crab burrows from invaded sites over that period, that many migrating crabs are killed when passing through *Anoplolepis* supercolonies (the only source for recent red crab deaths in these areas in December 1998 was through the recent migration), and that high densities and diversity of seedlings are maintained at invaded sites over this period. We have not yet analyzed seedlings heights but our impression is that average seedling size increased markedly from 1997 to 1998 (see also Plate 2H).

Use of canopy trees by *Anoplolepis*

Procedures. We surveyed activity of this ant on the boles of canopy trees (defined as those trees with >20 cm DBH) to assess tree canopy use by *Anoplolepis*. We used a four-scale rating system: heavy use (1000s of ants streaming up and down), moderate use (100s of ants), little use (10s of ants), and no use. At invaded sites at the Dales, Dolly Beach, and Hidden Valley we walked randomly through the site, locating a total of 100 canopy trees at each site. Each tree encountered was identified and an ant activity rating assigned. We made occasional observations of ants on the boles of the trees, noting prey items being carried and the direction of movement. We further observed whether *Anoplolepis* moving down the bole had distended, translucent abdomens, an indication of feeding on honeydew or

nectar in the tree canopy. We also collected samples of scale insects from 18 tree species for further identification. During observations along The Dales-Martin Point Track and in Hidden Valley, we also tallied and identified dead canopy trees as we encountered them.

Results and observations. At invaded sites at Dales, Hidden Valley, and Dolly Beach, *Anoplolepis* foraged heavily on almost all canopy trees (Figure 7). Of a total of 300 trees that were sampled, only 4 trees (1.5%), all at Dolly Beach, lacked crazy ants. Tree use indices at The Dales and Hidden Valley were extremely high: most canopy trees sampled at those sites had the highest use rating (83% and 68%, respectively). At Dolly Beach, canopy use was slightly lower, and only 24% of trees showed heavy use by *Anoplolepis*. Ant foragers moving down the boles of trees usually had distended translucent gasters; those moving upwards did not. Aside from our observations of *Anoplolepis* nesting in tree hollows on *Syzgium nervosum, Ochrosia ackeringae, Inocarpus fagifer,* in a bird's nest fern (*Asplenium nidus*), and on *Arenga* palms, further anecdotal evidence suggests that *Anoplolepis* nests in the canopies of some trees. We noted aggregations of *Anoplolepis* workers on boles of four tree species (*Celtis timorensis*, *Inocarpus fagifer*, *Syzgium nervosum*, and *Barringtonia racemosa*) returning prey items to their nests. In 4 of 7 observations, these aggregations moved consistently up the tree bole, suggesting these ants were returning prey items to nests located up the tree.

Most tree species at all *Anoplolepis*-invaded sites had infestations of scale insects. This was indicated by (1) the large numbers of scale that we encountered on saplings in the understorey and coppice shoots of bigger trees, (2) the repeated observation that *Anoplolepis* foraging downwards on the boles of almost all trees had distended gasters, a strong correlate of honeydew feeding (Haines *et al.* 1994), and (3) the widespread occurrence of sooty moulds on leaves and stems, which only occurs when a sugar substrate is present on plant surfaces (Bach 1991, Mibey 1997). Outbreaks of the lac scale insect *Tachardina*

?*aurantiaca*, in particular were associated with supercolony formation of *Anoplolepis gracilipes*. This honeydew-producing scale is native to Southeast Asia, is a host generalist, and is tended by a variety of ants on Christmas Island, including *A. gracilipes*. In rain forest on Christmas Island we have found it associated with at least 18 different tree species, including almost all canopy dominants.

Interestingly, both trees and saplings of nitrogen-fixing legumes (*Pongamia pinnata* along the Dolly Beach Track and *Inocarpus fagifer* in Hidden Valley and along The Dales-Martin Point Track) were heavily infested and affected by *Tachardina* ?*aurantica* in areas of *Anoplolepis* invasion (Plate 2A). However, dieback was not observed on *Erythrina variegata* (Fabaceae) on the shore terrace north of Martin Point. *Inocarpus fagifer* is typically a dominant seedling in many plateau and terrace forests (Green *et al.* 1997a,b). Indeed, 24% of all seedlings we censused on control, uninvaded plots were *I. fagifer* (Figure 6). But, we encountered only 10 seedlings of *I. fagifer* (0.1% of all seedlings) in plots in *Anoplolepis*-invaded forests. Further, saplings of *I. fagifer* in these invaded areas were heavily infested with scale and sooty mould; many dead stems were present. Deaths of canopy trees of *Inocarpus* also occurred disproportionately to those of other species at ant-invaded sites (at The Dales, χ^2 = 17.85, P < 0.001, Chi-square test; at Hidden Valley, χ^2 = 17.71, P < 0.001, Fisher exact test). At The Dales, 83% (15/18) of all standing dead canopy trees were *Inocarpus* while they comprised only 28% (28/100) of canopy trees sampled at random. Similarly, *Inocarpus* comprised all standing dead trees observed at Hidden Valley (6/6) while they made up only 22% of canopy trees sampled at random.

This dieback is consistent with the high levels of scale infestation and *Anoplolepis* use of *Inocarpus* we observed at both sites. Indeed, the frequency of occurrence of the highest rating of canopy use by *Anoplolepis* was significantly higher on *Inocarpus* than other

species at both the Dales and Hidden Valley (Dales, $\chi^2 = 5.49$, P < 0.001; Hidden Valley, $\chi^2 = 4.90$, P < 0.001, Fisher exact tests).

Known and projected impacts of *Anoplolepis gracilipes* on island forest ecosystems

We have presented strong evidence that invasion by *Anoplolepis gracilipes* causes rapid changes in forest structure and ecosystem processes. In essence, the island forest ecosystem is "reconfigured" in areas of *Anoplolepis* invasion. These effects of *Anoplolepis* are likely to expressed through at least three pathways (Figure 8): (1) through its elimination of the red land crab, (2) through its close association with honeydew-secreting scale insects, and (3) through its direct effect on other fauna on the forest floor and in the tree canopies.

(1) *Anoplolepis* kills and eliminates the dominant native animal, the red crab (as well as other land crabs) in areas of invasion. If we assume a density of one red crab per m² in island rain forest (a conservative estimate for shore terrace forests) and supercolony formation by *Anoplolepis* over 250 ha at present (Table 2), then it is likely that this ant has killed the approximately 2.5 million red crabs that formerly resided in ant-invaded areas over the last several years. Given various estimates for island-wide crab numbers (Hicks 1985, Morris and Adamczewska 1996), this should represent somewhere between 2 and 3.5 percent of the total red crab population. Overall abundances of blue crabs and robber crabs are not known, but deaths are likely to be at least in the thousands within the known areas of ant invasion.

Since *Anoplolepis* also kills massive numbers of migrating red crabs as they move through areas of supercolony formation (e.g., Dolly Beach Track, Greta Beach area, Dales-Martin Point area, Winifred Track – see above), both the percent mortality and spatial extent of impact on red crabs is underestimated. Since few crab burrows were found in invaded areas in 1998, it is likely that almost all of the dead red crabs we observed on the forest floor were migrating crabs. If so, *Anoplolepis* not only kills the resident land crab population but

depletes red crab populations from other, uninvaded areas when they migrate through supercolonies. Consequently, strong impacts on forest structure and processes could be felt in areas remote from areas of supercolony formation and ant impact on crabs in one location may "ripple" through other, uninvaded areas. Indeed, this appears consistent with decreasing crab and burrow densities over the last three years in our long-term study site near Murray Hill (Green *et al.*, unpublished results).

Although most of the results we present here are comparative, when considered alongside our long-term, manipulative experiments that removed crabs (Green *et al.* 1996, 1997a, b, in press), the results are compelling. Clearly, most of the "cascading" effects we found in this study were mediated through deletion of the dominant animal on the forest floor – the red land crab – by invasive ants. Basically, removal of the red crab results had two direct effects: increased seedling density and diversity, and an increased amount of standing litter on the forest floor (Figure 8A). As seedlings grow and litter accumulates, this in turn alters forest structure, both in light gaps and the shaded understorey.

(2) Although deletion of the red crab from invaded areas has marked impacts on forest structure and process, the effects of invasive *Anoplolepis* are manifold and go well beyond the effects cascading from their elimination of the red crab (Figure 8B). Crazy ants, wherever they have been studied, have been shown to be intimately associated with scale insects, which they tend for honeydew production (Van der Groot 1916, Haines *et al.* 1994). This can lead to scale outbreaks, as we have seen in all invaded areas, sooty mould formation, and dieback of subcanopy and canopy trees, especially *Inocarpus fagifer*. Thus, through mutualism with scale insects, *Anoplolepis* can indirectly lead to canopy dieback in areas where supercolonies form. Indeed, the large numbers of standing dead canopy trees of *Inocarpus fagifer* at the Dales and Hidden Valley are consistent with this viewpoint.

(3) *Anoplolepis* ants have an extremely broad dietary range, occur at extraordinarily high, sustained densities, and forage in three-dimensions. Unlike red crabs, which they displace, crazy ants forage in the rain forest canopy as well as on the forest floor. Further, in addition to nesting in crab burrows and woody debris on the forest floor, they frequently nest at the bases of canopy trees, in tree hollows, in epiphytes, and in the leaf axils of palms. We have also provided indirect evidence that they forage intensively and nest in canopies of forest trees. Given the observations of impacts of *Anoplolepis* on both invertebrates and vertebrates we have outlined above, their potential direct threat to a variety of vertebrate species of conservation value on Christmas Island (Table 4) is very large.

We can offer only anecdotes and observations that *A. gracilipes* directly threatens species (other than the land crabs and canopy tree species we describe above) of conservation value on Christmas Island. Nevertheless, these observations warrant serious attention. For example, L. Lumsden (pers. comm.) describes the death of a Pipistrelle bat, the only species of insectivorous bat on the island and recently listed as endangered, in a bat trap in 1998. The trap was set on The Dales-Martin Point Track, approximately 300 m west of the car park. This is in the middle of the *Anoplolepis* supercolony we identified in November 1997. Lumsden indicated that

> "…There were lots of ants on the ground, covering everything, and had
> covered the bat which by the time we found it was dead. I didn't pay much
> attention to the ants themselves at the time, but from memory they were
> pale-ish orange colour. Because the bat was confined in the trap it was
> unable to escape from the ants, and I am concerned that the same thing
> might be happening to the bats when in their roosts during the day."

She also describes the primary roosting sites of the Pipistrelle as under the exfoliating bark of *Tristiropsis acutangula*, in tree hollows of *Syzgium nervosum*, and under loose dead fronds of *Arenga* palms (Lumsden 1999). Our ant use indices of these tree species by *Anoplolepis* at The Dales, Hidden Valley, and along the Dolly Beach Track were among the highest we found (see Figure 7). We also found *Anoplolepis* nesting in tree hollows of *S.*

nervosum near Stronach Hill and along the Dolly Beach Track. Lumsden further reports that the numbers and distribution of Christmas Island Pipistrelle have declined markedly over the last decade. One of the strongest factors explaining the abundance of the pipistrelle was distance to the shore: fewer bats were found in coastal areas. *Anoplolepis* supercolony formation currently is greatest in shore terrace forests (Figure 1A, Table 2).

Harold Cogger (pers. comm.) has also expressed concerns about the potential impact of *Anoplolepis* on endemic lizards. In surveys of the reptiles of Christmas Island in June 1998, he reported a significant decline in the range of several species, including the endemic blue-tailed skink (*Cryptoblepharus egeriae*), since the previous survey in 1979. Further, none of the previous observations of the endemic gecko (*Lepidodactylus listeri*) made in 1979 were duplicated in his 1998 survey: no individuals were recorded. Cogger offers two hypotheses to explain island-wide shifts in range and declines in numbers of these endemic species. The impact of the El Nino drought of 1997 on canopy-dwelling *Lepidodactylus listeri*, and the direct or indirect impacts of *Anoplolepis* invasion. We saw *Anoplolepis* workers carrying a dead skink along The Dales-Martin Point Track, but do not know if they killed this lizard or were scavengers. These kinds of observations are especially disconcerting given Haines and Haines' report from the island of Mahé in the Seychelles. A one-hour search they conducted at Glacis, a site not invaded by *Anoplolepis gracilipes*, revealed over 100 individuals of the endemic skink, *Mabuya sechellensis*, whereas around Maldive, where crazy ants were numerous, a two-hour search produced less than 10 skinks (Haines and Haines 1978a).

Paul Meek (pers. comm.) also reported that ants, probably *A. gracilipes*, were a continual problem in use of hair tube traps to assess the occurrence of the Christmas Island Shrew.

Of course, the longer-term effects of *Anoplolepis* on Christmas Island rain forest are difficult to predict. One possible consequence is that its invasion will reduce "biotic resistance" to additional invaders, and secondary invasions will occur in areas with supercolonies. The likelihood of successful invasion depends on the attributes of both the invader and the characteristics of the recipient community. We have argued elsewhere (Lake and O'Dowd 1991, Green *et al.* 1997a) that the rain forests of Christmas Island are remarkably resistant to invasion and have attributed much of this resistance to the abundance of omnivorous red crabs which act as a barrier to would-be invaders. However, in *Anoplolepis*-invaded areas, red crabs are eliminated. Thus, we would expect that some potentially invasive species would now have higher probabilities of establishing in the rain forest. We are unable to predict which exotic species might establish, but several weed species along The Dales-Martin Point Track have now moved off from the edges of tracks, where they typically occur, and established profusely well into the rain forest.

The status of invaders, like *Anoplolepis*, and invaded sites can change through time. Following the accidental introduction of *A. gracilipes*, it took at least 50 years before populations grew explosively to cause extensive impact on the island's rain forest. Reasons for *Anoplolepis* remaining a "sleeper" for so long are unclear, but this pattern is common among introduced species (Kowarik 1995). Initiation of outbreaks and spread could be related to longer-term weather events, storms, or even to the accidental introduction of mutualist scale insects, like *Tachardina* ?*aurantica*, that may be necessary for sustaining high foraging activities of workers. Elsewhere, there is some suggestion that populations of *Anoplolepis* can "boom and bust." This may be the case on the island of Mahé in the Seychelles (Haines *et al.* 1994), perhaps in the lowlands of the island of Hawaii (F. Howarth, pers. comm.), and on the islands of Rodriquez and Agalega (Indian Ocean)(Haines *et al.* 1994). Nevertheless, these reports are anecdotal and the mechanisms for population decline

need to be identified. But we know that high, sustained densities of crazy ants can persist at sites for two or more years, the duration of our observations along The Dales-Martin Point Track, above Greta Beach, and at Tait Point.

If declines occur, they could be related to many factors, including disease, parasitism, and predation. However, it is possible that decline is related to local resource depletion following ant population outbreak, scale insect population outbreak, canopy dieback and scale population collapse, and reduction in the availability of ant nest sites. If so, our concern is that the "resources" depleted (and perhaps ultimately deleted, at least in areas of supercolony formation) may be conservation components (i.e., vulnerable and endangered species) or key functional components of the rain forest (e.g., the red crab). Whatever the temporal scale of boom and bust of ant dynamics in the future, we can already identify impacts on invaded island rain forest that will persist for decades to come.

Management of spread and mitigation of impact of invasion by *Anoplolepis*

Our goal in this section is to evaluate tactical and strategic aspects for control of *Anoplolepis* in rain forest on Christmas Island. First, we evaluate "tactics" for ant control, from chemical applications to biological control. Second, we consider "strategic" options for control, from complete eradication to no action. Lastly, we make recommendations for research and management efforts.

Control methodologies

Chemical control. Chemical control of ants involves the use of contact sprays, dusts, as well as toxic baits. Effects of contact sprays and dusts may be limited to foraging workers and have limited effects on brood production. Usually, toxic baits are usually considered most effective under field circumstances. Broadcast treatments using toxic baits are advantageous in that ant foragers ingesting the bait return to the colony and, through trophallaxis (oral transfer of liquid food), pass the poison among other workers, among

brood, and to the queen. If toxic effects on foragers are not immediate, this can result in the death of brood and the killing or sterilizing of queens, thus eliminating entire colonies. Because large areas can be treated, this method can also slow down reinfestation by the migration of colonies from uninfested areas.

Nevertheless, the chemical option remains controversial in natural areas because of potential persistence in the environment and non-target impacts. This is of special concern on islands that have many endemic species with high conservation value. For example, formulations that make baits attractive to invasive ants often attract non-target native ant species. This may not be a serious problem on Christmas Island, which may lack native ants entirely (R.W. Taylor, pers. comm.), but baits may be particularly attractive to other arthropods, including a variety of terrestrial crabs. Many bait formulations in current use (e.g., hydromethynon) have relatively high LD_{50} for vertebrates, but we know of no studies that examine their toxicity to Crustacea.

In the Seychelles in the 1970s, toxic baits, using chlorinated hydrocarbons (Aldrin), were developed for the control of *Anoplolepis*, and proved more effective than chemical spray treatments (Haines and Haines 1979a,b,c). The toxic baits effectively controlled ant nuisance in agriculture and around homes, killing more than 90% of *Anoplolepis* in the first few days (Haines and Haines 1979b). However, *Anoplolepis* numbers recovered after 3-12 months, probably through re-invasion from untreated areas. Rate of recovery of ant population appeared to depend on size of area baited. When a 2 ha area was baited, 50% recovery of *Anoplolepis* took about 85 days; when a 50 ha area was baited, 50% recovery took over 300 days. However, baiting was most effective in built-up areas relatively free from vegetation.

A variety of toxic principles have been used in ant baits. In the past, chlorinated hydrocarbons were widely used as toxic baits; however, most of these are no longer

considered safe for use and have been deregistered. The toxic principles in ant baits include the so-called "stomach" poisons, hydramethylnon (Maxforce, Amdro), sulfuramid, and sodium tetraborate decahydrate (Borax). Insect Growth Regulators (IGRs) disrupt development and include compounds such as methoprene and fenoxycarb (Williams 1994). Stomach poisons work relatively fast compared to IGRs, but may sometimes work too quickly, thereby eliminating workers before the insecticide can be distributed throughout the entire colony. One promising approach is to use pheromones (compounds produced by a species that regulate their own behaviour) as "biopesticides" to disrupt the reproduction by the queen (Vargo 1996). However, this would first require development of a large research base for the ecology and chemical bases for the behaviour of *Anoplolepis*.

Biological control. The biological control of *Anoplolepis* by means of a self-sustaining and host-specific parasite would be more desirable than almost any other type of control program. Potential control organisms for invasive ants include bacteria, entomophagous fungi, protozoans, nematodes, and insects (Williams 1994). Unfortunately, few pathogens and parasites have been described in the literature for ant species other than fire ants and leaf-cutting ants (Williams 1994). Because Christmas Island appears to lack any native ant species, biological control remains a feasible long-term option for control of the crazy ant. However, start-up costs for such a program would be very large, including surveys of natural enemies of *A. gracilipes* in other areas (Van der Groot 1916 cites several natural enemies of *Anoplolepis*, including mites and a tachinid fly, in Indonesia), taxonomic studies, studies of the basic biology of selected natural enemies, extensive host-specificity tests of the control organisms, petition and approval for release, release and augmentation, followed by post-release monitoring studies. Delivery of a single species for introduction could take a decade or more. The only biocontrol effort involving ants of which we are aware involves the introduction of phorid flies of the genus *Pseudaceton* to control the red

imported fire ant, *Solenopsis invicta*, in the United States. This effort is controversial because of concerns about non-target impacts on native ant species by the phorid fly (Gilbert 1996).

A possible alternative to direct biological control of *Anoplolepis* would be to target scale insects for biological control, if indeed, *Anoplolepis* supercolony formation depends on high densities of scale insects. We suspect this is so, but it remains to be demonstrated. A large literature exists on the natural enemies of scale insects and some successful control efforts are known (Ben-Gov and Hodgson 1997); however, nothing is known about how and whether scale control influences numbers of associated ants. In any case, a much better understanding of scale-*Anoplolepis* interactions is first necessary.

Control strategies

1. Eradication. We know of no successful long-term eradication of introduced ants on any island. Given the spatial scale of the problem, the broad "niche" of the crazy ant, its wide distribution on Christmas Island, the inaccessible and difficult terrain in many known areas of infestation, and the probable cost of a sustained, island-wide effort, we feel that eradication of *A. gracilipes* is an unrealistic goal.

2. Population depletion. Significant depletion, i.e., reduction in current population densities of *Anoplolepis* allowing recovery of land crab populations and re-establishment of "normal" forest processes, may be a difficult but achievable goal. This outcome could be attempted through the broadcast of toxic baits (see above) throughout areas of infestation. However, past control efforts on Mahé in the Seychelles showed that, although a single application of toxic baits markedly reduced *Anoplolepis* populations, ants re-established within 3-12 months, depending on the area baited (Haines and Haines 1979b). This suggests that any attempt at long-term reduction of ant densities across Christmas Island will require multiple applications per year; however,

without an understanding of longer-term dynamics of supercolonies, we do not know for how long it would be necessary to sustain such an effort. Given the current costs of commercial toxic baits, such a program would prove costly.

3. <u>Containment</u>. *Anoplolepis* supercolony formation could be confined to existing areas. This would require active defence, through chemical baiting, of the perimeter of infestations. A common strategy in control of invasive plants is to target "satellite" (small outlying) infestations first and once these have been contained, redirect efforts towards "core" (large, central) infestations. Of course, this assumes that a thorough and current survey of the distribution and abundance of the invader is available. In practice, this would means setting priorities for control among different areas of ant infestation. Using a containment strategy presents some difficulties, including the high rate of spread of *Anoplolepis* and our current inability to predict the location of new infestations. This is probably a less expensive option than population depletion in that the perimeters alone could be baited to prevent supercolony expansion. This may require that some drill lines be re-opened for access to contain *Anoplolepis* supercolonies. If populations of *Anoplolepis* do boom and bust, then confined supercolonies could dissipate.

4. <u>Special Ecological Areas</u>. In the event that containment of *Anoplolepis* supercolonies across the island proves infeasible, control efforts could be directed towards maintaining "Special Ecological Areas" (SEAs) free of crazy ant infestations. An expert panel, possibly based on the Christmas Island Recovery Team, could develop criteria for selection of SEAs. Criteria, for example, could include the absence of crazy ant supercolonies, the conservation value of an area, the presence of "defendable" edges (e.g., major roads, minefields) that may act as barriers to ant dispersal, and the presence of red crab migratory pathways. The two former Scientific Reference Areas (Egeria and

Middle Points) could also be considered as possible SEAs. Once several SEAs are established, a monitoring program would be initiated to detect *Anoplolepis*. If crazy ant infestations were detected, rapid deployment of toxic baiting would commence in infested areas, followed by monitoring for effectiveness.

5. <u>No action</u>. No action, as a control policy, would rely completely on the rapid dissipation of *Anoplolepis* supercolonies through time, without human intervention. This risks possible extinction of many already vulnerable and endangered species on the island, widespread ecosystem degradation, changes in forest species composition, altered ecosystem processes, and higher probabilities of forest invasion by a variety of non-indigenous plants and animals.

Research and management recommendations

The recommendations outlined below are aimed at the following outcomes.

- Avoidance of extensive ecosystem disruption on the island, primarily by preventing (a) massive reduction in numbers of endemic land crabs that largely regulate forest regeneration and ecosystem processes and (b) canopy dieback as a result of scale insect outbreaks.

- Prevention of massive population reductions, if not extinctions, of island endemic species, including vulnerable and endangered seabirds, land birds, reptiles, and mammals.

- Maintenance of natural history tourism as one base for the island economy.

R1. <u>Establish the spatial scale and tempo of ant invasion</u>. A systematic survey of the distribution and abundance of *Anoplolepis gracilipes* is required across the island. Survey will also be necessary outside National Park jurisdiction since *Anoplolepis* does not respect park boundaries. Repeated surveys are necessary to determine the island-wide dynamics of spread. These surveys should be designed so that they can be

integrated into and build upon the existing Christmas Island Geographic Information System. A survey (and subsequent monitoring) system should include a maximum of one km^2 grid of permanent sampling points. The existing drill line system could be used for access on the plateau and higher terraces.

R2. <u>Analyze the dynamics of *Anoplolepis* populations, ant-scale interactions, and their role in understorey and canopy dieback</u>. These studies will determine the temporal stability of invasive ant and scale insect populations, rates and means of *Anoplolepis* spread, and direct impact of ants on the forest understorey and canopy. This information is central in the production of designs for control and containment efforts and impact assessment.

R3. <u>Assess the direct impact of *Anoplolepis* on the dominant red land crab, and the indirect effects of red crab removal on forest structure and processes</u> (i.e., ecosystem "integrity"). The red crab could be considered as a "keystone" species whose activities govern the well-being of many other native island species. Because the red crab is central in the island food web, studies that monitor the impact of its deletion from the ecosystem will identify the nature, rate, and scale of ecosystem change, information necessary to determine the magnitude and effectiveness of control/containment efforts for *Anoplolepis*.

R4. <u>Assess the impact of this invasive ant on a subset of island species of concern, including selected endemic reptiles, seabirds, land birds, and mammals</u>. Currently, information on the direct effects of *Anoplolepis* on all animals, other than land crabs, is circumstantial. These results will inform on the likely impact of invasive ants on Christmas Island endemic fauna and species and forms listed as threatened under various authorities (e.g., ANZECC, ESP Act). The Christmas Island Recovery Team, or some other expert panel, could nominate species for impact studies.

R5. <u>Establish a control program based on toxic baits directed towards control and containment of *Anoplolepis gracilipes* in rain forest on Christmas Island</u>. Of available options, chemical control will have a shorter start-up time, a critical consideration when *Anoplolepis* invasion is expanding apace. Initially, we suggest that existing commercial formulations of toxic baits (e.g., hydromethynon baits) be evaluated. Two baiting tactics should be considered: one in existing infested areas (where non-target effects may be less of an issue) and the other along the boundaries of infested areas (where non-target impacts are likely to be more important). Both target and non-target effects should be included in initial studies of bait effectiveness. These strategies will inform on the feasibility of population depletion, containment, and restriction strategies (see above).

R6. <u>Develop contingency plans to focus control efforts on restricted, "Special Ecological Areas" (SEAs)</u>. Establish an expert panel, possibly based on the Christmas Island Recovery Team, to develop criteria for selection of SEAs. Criteria, for example, could include the absence of crazy ant supercolonies, the conservation value of an area, "defendable" edges (e.g., major roads, minefields) that may act as barriers to ant dispersal, and the presence of red crab migratory pathways. The two former Scientific Reference Areas (Egeria and Middle Points) could also be considered as possible SEAs. Once several SEAs are established, develop a monitoring program to detect *Anoplolepis* incursions.

R7. <u>Consider *Anoplolepis* invasion in the broader management plans for Christmas Island National Park</u>. Revisit approved, pending, and draft Recovery Plans for threatened species under the Endangered Species Protection Act in light of potential impacts of the crazy ant. Incorporate impact assessment and mitigation of *Anoplolepis* invasion in any revision of the Christmas Island National Park Plan of Management. Provide

information to residents and workers on Christmas Island to minimize unintended transport of *Anoplolepis* from infested to uninfested areas. Use the *Anoplolepis* invasion to illustrate the advantages of prevention of entry, through a strict, effective quarantine service, as the best strategy to prevent future pest problems on the island.

Comments on costs of a research and management program

Below we give some estimates of the resources we believe necessary to initiate a research and management program for *Anoplolepis gracilipes*. Resources are divided under three subprograms: survey, impact assessment, and control. The scale of effort we describe would be comparable to other major research and management programs carried out on the island (e.g., current forest rehabilitation program and the Abbott's Booby program). We estimate annual recurrent costs in the vicinity of $500-600K per year.

Anoplolepis survey:

1.5 personnel (salaries and on-costs), computer, high quality GPS unit, GIS software, one vehicle, office space.

Impact assessment:

1.75 personnel (salaries and on-costs), computer, one vehicle, office space

Control:

1.75 personnel (salaries and on-costs), computer, baiting supplies, one vehicle, office space. In addition, commercial baiting supplies could cost upwards of $400 per hectare per application, tax-free.

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Table 1. The crazy ant, *Anoplolepis gracilipes*. Description is courtesy of the Japanese Ant Database (Dr. Hirotami Imai). Also see Plate 1.

Anoplolepis gracilipes (Fr. Smith)   Common names: crazy ant, yellow crazy ant, long-legged ant

Synonyms:

    Formica longipes Jerdon (Jerdon, 1851)

    Plagiolepis longipes Emery (Emery, 1887)

    Anoplolepis (*Anoplolepis*) *longipes* Emery (Emery, 1925)

Description:

Total length of workers around 4 mm. Body color yellow, gaster brownish. Antennae and legs remarkably long. Head oval. Clypeus produced medially, with convex anterior margin. Eyes relatively large and produced. Mandibles with 8 teeth. Antennae 11-segmented; scapes twice as long as the length of the head, or longer; their second to terminal segments each more than three times as long as wide. Mesosoma slender. Pronotum narrow, with almost straight dorsum in profile. Anterior portion of mesonotal dorsum, back to the propodeum, gently concave in profile. Propodeal dorsum convex in profile. Petiole thick, with a reverse U-shaped node. Erect hairs present on head and gaster, lacking on dorsum of mesosoma.

Table 2. Locations, areal extent, and estimated ages of supercolony formation by *Anoplolepis gracilipes* on Christmas Island, Indian Ocean determined in November/December 1998. Established infestations were defined as areas where supercolony formation had clearly occurred and probably persisted for at least two years. Recent infestations, in which crazy ants occupied red crab burrows and were abundant on the ground, probably originated in the last year. "Extinct" infestation indicates a location where a supercolony was reported previously but could not be relocated in our survey. See Figure 1A.

Area	Location	Extent/Age
Established infestations		
Winifred	1.1 km back from Winifred Beach Carpark in crab migration pathway.	Not surveyed accurately but at least several hectares. ~ 1 year.
Dales-NW Pt-West White Beach	Entire shore terrace from 2WD carpark at the Dales, to Martin Pt through to NW Pt, and east to West White Beach. This infestation extends up the West White Beach track, from the shore terrace to about the 170 m contour. Above the shore terrace, the width of the infestation is unknown. We assumed to extend at least hundreds of meters either side of track.	Approximately 100-150 ha. > 2 years.
Below Central Area Workshop	Base of the first inland cliff down to at least the 70 m contour.	Not surveyed accurately but at least several hectares. Age unknown.
Greta Beach Area	Shore terrace from 200 m north of carpark to 300 m south of carpark.	Approximately 10 ha. > 2 years.
Dolly Beach Track	Shore terrace along the Dolly Beach track, beginning 300 m from beach and extending for about 1.2 km north towards the Dolly Beach carpark.	Approximately 25 ha. > 2 years.
Hidden Valley	Terrace (c. 200 m ASL) east of Field 17 at the bottom of the switchback, extending southward for at least 300 m. This infestation extends northwards several hundred meters to the scree slope dropping down to another terrace, approximately 30-40 m below (160-170 m ASL). Infestation extends at least several hundred meters further north along this lower terrace. Note that this infestation is almost directly west to that along the Dolly Beach Track.	Not surveyed accurately but probably near 15 ha. > 1 year.

Area	Location	Extent/Age
Established infestations (cont.)		
Tait Point/ Andrews Point	The first infestation occurs about 2.6 km southwest of the gate to the Boulder Track, beginning several hundred meters north of Tait Point and extending 1.2 km further south. The second infestation begins several hundred meters south of Andrews Point and extends approximately 300 m, ending 400 m north of the Boulder near South Point.	Approximately 30 ha. > 2 years.
South Point Powerline Track	Infestations in forest either side of road for 1.9 km, from 1.8 km north of old station to 3.7 km north of old station. This infestation aligns well with the larger of the two infestations on the shore terrace below, suggesting the forest from shore to plateau, may be invaded.	Inspection only possible within 20 m of each roadside. At least 8 ha. Age unknown.
Incipient infestations		
Murray Hill study site	Green, O'Dowd and Lake long-term study site just below the road to NW Point, about 1 km east of the West White Beach track.	Not surveyed accurately but at least several hectares. < 1 year.
Near Field 22S	Primary forest at southern edge of Field 22S, at that point on the circuit road where it kinks around the field.	At least one hectare in extent. < 1 year.
Stronarch Hill	Plateau "shoulder" to the east of Stronach Hill, above Greta Beach. Infestation from the 220 m contour down to at least 150 m contour.	Not surveyed accurately but at least several hectares. < 1 year
"Extinct" infestation		
Phosphate Hill	Below (north) the rock crushing plant and to the east of Taman Sweetland, about 180 m ASL. First seen in 1989 by J. Tranter and P. Green, but could not be located again in 1998. Possibly destroyed by recent mining activity. Area never assessed, but at least 1-2 ha in extent.	--

Table 3. Analysis of variance comparing measures of (A) ant activity, (B) crab abundance and mortality, (C) litter cover, and (D) seedling density and diversity between plots in areas of supercolony formation by the exotic ant *Anoplolepis gracilipes* and in uninvaded, control areas. Variables in (A) and (B) were square-root transformed. Untransformed data were used in analysis of percent litter cover (C). In (D), seedling density was square-root transformed, and untransformed values were used in analyses of species richness and diversity.

Source	df	SS	MS	F	P
(A) Ant activity					
Anoplolepis activity index					
Invasion	1	11.081	11.081	45.400	0.001
Block	5	0.961	0.192	0.788	0.600
Error	5	1.220	0.244		
Other ant activity index					
Invasion	1	0.950	0.950	7.334	0.042
Block	5	1.363	0.273	2.105	0.217
Error	5	0.648	0.130		
(B) Crab abundance					
Dead crabs (no. dead crabs/80 m^2)					
Invasion	1	103.186	103.186	18.808	0.007
Block	5	27.432	5.486	1.000	0.500
Error	5	27.432	5.486		
Crab burrows (no. burrows/80 m^2)					
Invasion	1	196.868	196.868	44.827	0.001
Block	5	21.828	4.366	0.994	0.503
Error	5	21.958	4.392		
(C) Litter cover					
% Litter cover					
Invasion	1	0.580	0.580	21.427	0.006
Block	5	0.150	0.030	1.110	0.435
Error	5	0.135	0.027		
(D) Seedling density and diversity					
Density (no. seedlings/80m^2)					
Invasion	1	2800.300	2800.300	123.590	0.000
Block	5	78.767	15.753	0.6953	0.650
Error	5	113.290	22.658		
(E) Species richness (no. spp./80 m^2)					
Invasion	1	752.080	752.080	34.057	0.002
Block	5	145.750	29.150	1.320	0.384
Error	5	110.420	22.083		
(F) Species diversity (Simpson's index of diversity)					
Invasion	1	7.358	7.358	7.957	0.037
Block	5	23.891	4.778	5.167	0.048
Error	5	4.623	0.925		

Table 4. Notable vertebrate and crustacean species in rain forest on Christmas Island threatened directly in areas of supercolony formation by the exotic ant *Anoplolepis gracilipes*. Endemics species are indicated by '*,' endemic subspecies or forms by '†.' ANZECC threatened species listed as "Vulnerable" (species which will probably become endangered if it continues to be threatened) or "Endangered" (species which is in danger of extinction and will probably not survive if it continues to be threatened).

Species	Status	Nest sites/Habitat
Seabirds		
Golden Bosunbird	Endemic[†]	Treeholes, inland cliff
Red-footed Booby	--	Canopy
Abbott's Booby	Endemic[*], Endangered	Canopy
CI Frigatebird	Endemic[*], Vulnerable	Canopy
Common Noddy	--	Canopy, cliffs
Land birds		
Imperial Pigeon	Endemic[*]	Canopy, subcanopy
Emerald Dove	Endemic[†]	Shrubs
CI Hawk-Owl	Endemic[*], Vulnerable	Subcanopy treehole
CI Goshawk	Endemic[†], Vulnerable	Canopy
CI Thrush	Endemic[†]	Shrubs
CI White-eye	Endemic[*]	Shrubs
Mammals		
CI Pipistrelle Bat	Endemic[*,] Endangered[a]	Under tree bark, treeholes
CI Fruit Bat	Endemic[*]	Canopy
CI Shrew	Endemic[*], Endangered	Litter, woody debris
Reptiles		
CI Blue-tailed Skink	Endemic[*]	Canopy gaps, treefalls
CI Gecko	Endemic[*], Vulnerable	Canopy
CI Blind Snake	Endemic[*], Vulnerable	Soil
Crustaceans		
Red Crab	Endemic[*]	Forest floor
Robber Crab	--	Forest floor
Blue Crab	--	Forest floor, freshwater areas

[a]see Australian Bat Action Plan (draft, Table 1.1)

Figure legends

Figure 1. (A) Known areas of supercolony formation by the exotic invasive ant *Anoplolepis gracilipes* on Christmas Island, Indian Ocean, December 1998. CWB refers to the area below the Central Area Workshop. (B) Locations of six permanent study sites for impact of the crazy ant *Anoplolepis gracilipes* on rain forest, Christmas Island, Indian Ocean. Paired sites (invaded and control site) occur in and nearby areas of supercolony formation. Long-term crab exclusion experiments near Murray Hill (nine years) and the Blowholes (four years) are also shown. Note that the Murray Hill site has been invaded by *Anoplolepis*.

Figure 2. Comparison of impact of invasion by *Anoplolepis gracilipes* in areas of supercolony formation with uninvaded, control areas. (A) ant activity index at sugar baits, (B) crab mortality on the forest floor, (C) red crab burrow densities, and (D) percent litter cover. Means + standard error. N = 6.

Figure 3. Inverse relationship between occupation of red crab burrows by the invasive ant *Anoplolepis gracilipes* and the presence of live crabs. N is the number of burrows that were excavated.

Figure 4. Comparison of impact of invasion by *Anoplolepis gracilipes* on (A) seedling density, (B) species richness, and (C) species diversity (Simpson's Index of Diversity) in areas of supercolony formation and uninvaded, control areas. Means + standard error. N = 6.

Figure 5. Two-dimensional NMDS ordination of relative species composition of seedlings for all six areas, divided into invaded and control sites. Stress in two dimensions = 0.11. Analysis of Similarities showed that relative species composition of seedlings differed significantly between areas invaded by *Anoplolepis* and uninvaded, control areas (P = 0.009). Areas are: DA = The Dales-Martin Point, DB = Dolly Beach, GB = Greta Beach, HV = Hidden Valley, TP = Tait Point, and WI = Winifred Beach Track.

Figure 6. Relative abundance of seedling species pooled across invaded sites (n = 30 quadrats) and control plots (n = 30 quadrats) over all six areas. Species codes are as follows: AiC = *Aidia cochinchinensis*, AlC = *Allophyllus cobbe*, AlR = *Alchornea rugosa*, ArC = *Ardisia colorata*, AL = *Arenga listeri*, AT = *Acronychia trifoliolata*, BC =*Berrya cordifolia*, BR = *Barringtonia racemosa*, CI = *Claoxylon indica*, CN = *Cryptocarya nitens*, CP = *Celastrus paniculatus*, CR = *Carmona retusa*, CT = *Celtis timorensis*, DG = *Dysoxylum gaudichaudianum*, DP = *Dendrocnide peltata*, DS = *Dendrocnide sinuata*, GA = *Gyrocarpus americana*, GI = *Grewia insularis*, GS = *Guettarda speciosa*, HL = *Heritiera littoralis*, HO = *Hernandia ovigera*, IF = *Inocarpus fagifer*, KH = *Kleinhovia hospita*, LA = *Leea angulata*, MA = *Melia azedarach*, MC = *Maclura cochinchinensis*, MT = *Macaranga tanarius*, OA = *Ochrosia ackeringae*, PA = *Pipturus argenteus*, PE = *Pandanus elatus*, PF = *Pittosporum ferrugineum*, PG = *Pisonia grandis*, PL = *Premna lucidula*, PN = *Planchonella nitida*, PO = *Pachygone ovata*, PP = *Pongamia pinnata*, PU = *Pisonia umbellifera*, SE = *Schefflera elliptica*, SN = *Syzygium nervosum*, TA = *Tristiropsis actutangula*, TC = *Terminalia catappa*, VR = UNK = unknown.

Figure 7. Canopy tree species frequency (100 trees each > 20 cm DBH sampled at each of three sites) and use index by *Anoplolepis gracilipes*. *Anoplolepis* use index is described in the text. Dashed horizontal line on each bar graph is the overall tree use index calculated for each site. Species codes are as follows: AT = *Acronychia trifoliolata*, AL = *Arenga listeri*, BR = *Barringtonia racemosa*, BC =*Berrya cordifolia*, CN = *Cryptocarya nitens*, CT = *Celtis timorensis*, DG = *Dysoxylum gaudichaudianum*, DS = *Dendrocnide sinuata*, EJ = *Ehretia javanica*, FM = *Ficus microcarpa*, GS = *Guettarda speciosa*, HO = *Hernandia ovata,* IF = *Inocarpus fagifer*, LA = *Leea angulata*, MT = *Macaranga tanarius*, MA = *Melia azedarach*, OA = *Ochrosia ackeringae*, PN = *Planchonella nitida*, PP = *Pongamia pinnata*, PL = *Premna lucidula*, PU = *Pisonia umbellifera*, SN = *Syzygium nervosum*, TA = *Tristiropsis actutangula*, TC = *Terminalia catappa*.

Figure 8. Simplified interaction webs illustrating major interactions and their possible cascading effects in rain forest with and without the exotic invasive ant, *Anoplolepis gracilipes*. (A) Interaction web and cascading effects of the dominant red land crab (based on Green *et al.* 1997, in press). (B) Interaction web in areas of supercolony formation of the invasive exotic ant, *Anoplolepis gracilipes*. Because this ant kills and eliminates land crabs, the interaction web involving these crabs is deleted. '+ve' indicates a positive effect; '-ve' is a negative effect. Direct feeding interactions are indicated by solid lines. Dashed lines show indirect effects. Some possible changes in the tree canopy, litter fauna, and canopy fauna are illustrated (▼= decrease in abundance, ▲ = increase in abundance, and △= change in species composition).

Plate 1. The crazy ant, *Anoplolepis gracilipes* (Fr. Smith) (Hymenoptera: Formicidae). A. Top view of dorsal surface of a worker. B. Side view of a worker. C. Front view of head of a worker. Photographs are courtesy of the Japanese Ant Database (Dr. Hirotami Imai).

Plate 2.

A. The lac scale insect *Tachardina* ?*aurantiaca* being tended *by Anoplolepis gracilipes* on a sapling of the Tahitian chestnut *Inocarpus fagifer*. The stem is covered in sooty mould. Scale crawlers are indicated by the arrow.

B. *Anoplolepis* at a sugar bait placed at the invaded site along The Dales-Martin Point Track.

C. A berried female of the red land crab *Gecarcoidea natalis* under attack by *Anoplolepis gracilipes* (arrow) along The Dales-Martin Point Track.

D. Dead migrating red crabs (*Gecarcoidea natalis*) clustered at the base of a tree. Invaded site along the Winifred Beach Track.

E. Close up of a ¼m^2 quadrat at the uninvaded, control site along the Winifred Beach Track. Note the near absence of leaf litter.

F. Close up of a ¼m^2 quadrat at the invaded site along the Winifred Beach Track, above the car park. Note the recently dead red crab, the thick layer of leaf litter, and the presence of seedlings.

G. Uninvaded, control site along the Winifred Beach Track, above the car park. Note the open understorey, the near absence of leaf litter, and few seedlings – features characteristic of the rain forest on Christmas Island.

H. Invaded site along The Dales-Martin Point Track. Note the high density of large seedlings/saplings, especially *Dysoxylum gaudichaudianum*. A deep layer of leaf litter can be seen in the foreground.