The establishment of *Anolis wattsi* as a naturalized exotic lizard in Trinidad

G.L. White[1], Adrian Hailey[2]

[1] 16 Waterloo Estate, Carapichaima, Trinidad and Tobago, West Indies; e-mail: g-white@tstt.net.tt
[2] Department of Life Sciences, The University of the West Indies, St. Augustine, Trinidad and Tobago, West Indies; e-mail: ahailey@fsa.uwi.tt

Abstract. Trinidad has a single native *Anolis* species (*A. chrysolepis*) and several introduced exotics (*A. aeneus*, *A. extremus*, *A. trinitatis*, and *A. wattsi*). *Anolis wattsi* is the latest introduction, being first observed in the Waterloo area in 1992. This paper describes the distribution of this species in 2000 and 2004, by which time it had become established as a naturalized exotic lizard in western Trinidad. The species was verified as *A. wattsi* in the strict sense (formerly *A. wattsi wattsi*), differentiated from sibling species (other former subspecies of *A. wattsi*). *A. wattsi* is currently distributed in five discontinuous urban localities within an area of about 15×5 km, which suggests jump dispersal across unsuitable habitat (sugar cane fields). The rate of spread was about 100 m yr^{-1} within urban areas, and >1 km yr^{-1} for jump dispersal. *A. wattsi* occurred in the same habitat as the larger *A. aeneus* in gardens, parks and vacant lots. The two species differed significantly in perch height (but not in perch diameter) and substrate use. *A. wattsi* used lower perches, and replaced *aeneus* along the series trees (94% *aeneus*), posts and bushes, walls and fences, and ground (87% *wattsi*). Perch height of *A. aeneus* did not differ between locations with and without *A. wattsi*, and there was no correlation between numbers of the two species among sites. Possible interactions among introduced and native *Anolis* species on Trinidad are discussed.

Key words: *Anolis aeneus*; *Anolis wattsi*; Caribbean; competition; exotic; invasive; naturalized; perch height; Trinidad; West Indies.

Introduction

There has been a long history of naturalization (establishment of successful populations of an introduced species) of *Anolis* lizards, both between Caribbean islands and in the southern USA (Losos et al., 1993; Campbell, 2003; Lever, 2003). Introduced species in general present problems for native faunas and floras through competition, predation, herbivory and disease (McKinney and Lockwood, 1999; Mack et al., 2000); they are also of basic ecological interest as a model of natural colonization (e.g. Williams, 1969). Small islands with native *Anolis* lizards have either a single small to medium sized species, or one small and one large species (Roughgarden, 1995). Introductions of *Anolis* fail where there is already an ecologically similar species (Losos et al., 1993), and most successful introductions to islands have been of large species (Roughgarden, 1995). Introduced *Anolis* on Trinidad are of interest as there are several naturalized species, all of which are small.

Murphy (1997) lists four species of *Anolis* in Trinidad; *A.* (*Norops*) *chrysolepis planiceps* (Troschel), *A. aeneus* (Gray), *A. trinitatis* (Reinhardt and Lutken), and *A. extremus* Garman. Only *A. chrysolepis* is native to Trinidad, and is widespread in forests, into which the introduced species have not spread. *A. aeneus* is currently the most abundant anole in suburban gardens. This species is native to Grenada, where it occupies sites over a wide range of land use and disturbance, together with the large *A. richardii* (Germano et al., 2003). Published accounts of *A. aeneus* in Trinidad date back to 1900 (Murphy, 1997). *A. trinitatis* is native to St Vincent (where it occurs with the large *A. griseus*) and is also a long-standing naturalized species in Trinidad. *A. extremus* (a medium-sized species from Barbados) was released in small numbers on Huevos Island just off N.W. Trinidad (Boos, 1967, 1977) and specimens were also collected in Port of Spain in 1982 (Murphy, 1997). This appears to have been an unsuccessful colonist in Trinidad, although it is naturalized in St Lucia (Gorman, 1976). *A. chrysolepis* is the most terrestrial of the four species as it forages on the ground (Boos and Urich, 1986), the others being largely trunk-dwellers.

Anolis wattsi was discovered in Trinidad in November 1992 by G. White, in the grounds of the Caroni Research Station (Boos, 1996). This is an agricultural research station at Waterloo in west central Trinidad run by Caroni (1975) Limited. (1975 refers to the date the sugar company was purchased by the state — the research station itself was formed in 1959 as the Central Agricultural Research Station.) The lizards were particularly abundant within a patch of pineapple, including the cultivar “Black Antigua”. It was therefore suspected that planting material brought from Antigua was the source of the population. *A. wattsi* Boulenger is native to Antigua (Boulenger, 1894), where it occurs with the large *A. leachii*, and neighbouring islands (Schwartz and Henderson, 1991). Four subspecies have previously been recognised; *wattsi* on Antigua (and introduced to St Lucia), *pogus* on St Maarten, *schwartzi* on St Kitts, Nevis and St Eustatius, and *forresti* on Barbuda (Lazell, 1972; Schwartz and Henderson, 1991; Uetz, 1999). Recent taxonomic opinion is that at least *pogus* and *schwartzi* should be elevated to full species (Powell and Henderson, 2001; Schneider et al., 2001). We therefore use *A. wattsi* in the strict sense, as equivalent to *A. wattsi wattsi*, but include discussion of ecological studies on the other former subspecies in view of their similarity (Malhotra and Thorpe, 1999).

No surveys were performed to determine the range of the population upon its discovery in 1992, although it was believed to have been restricted to the grounds of the research station; no specimens were observed in the adjacent housing compound. The present study was performed in July 2000 and April-August 2004 to verify the identity of the species (in the strict sense, differentiating this from other former subspecies), and to determine its possible date of introduction, current range and rate and nature of spreading. We also examine the possible interactions with *A. aeneus*, a species already naturalized in the area, in terms of the spatial niche which may reflect competition among both native and introduced anoles (Losos and Spiller, 1999).

Materials and Methods

An attempt was made to determine the date of introduction of *A. wattsi* to Trinidad by examining correspondence at Caroni Research Station and interviewing persons involved in importation of plant materials. The records of the Trinidad and Tobago Plant Quarantine Service before 1992 were also examined for likelihood of importation, under four criteria: date; country of origin; item and quantity; relevance to Caroni Research Station. These criteria were scored for each import record as: likely (1); possible (0.5); or unlikely (0). The overall score for each record was the product of those of the four criteria. The scoring system was as follows. Date: likely = 1982-1991; possible = 1972-1981; unlikely = before 1972. Country of origin: likely = Antigua, St Lucia; possible = West Indies, Caribbean; unlikely = all other locations. Item and quantity: likely = plants or soil in sufficient quantity (50+ plants, 25+ kg of plant or geological material); possible = all other materials. Relevance to Caroni Research Station: likely = agricultural or horticultural materials; possible = all other materials.

A survey was conducted in July 2000 in the residential areas surrounding the Caroni Research Station in west central Trinidad (fig. 1), including Brickfield Village, Waterloo Road, Butler Village, Carapichaima, Orange Valley, and Union Village (fig. 2). The survey consisted of riding a bicycle at about 5 kph along all roads in the surveyed areas, and carefully examining the fences, ditches, trees or walls bordering the road. Each road was traversed twice to examine both sides, and all *Anolis* lizards observed were recorded. Visits were also made to six localities further from Waterloo (outside the area shown in fig. 2) which had received plants propagated at the research station: Brechin Castle, Todd's Road, La Gloria, Orange Grove, Tunapuna, and Fredrick Settlement. In October 2003 a photograph of *A. wattsi* was used on the cover of Living World, the journal of the Trinidad and Tobago Field Naturalists' Club. The caption requested readers to report any sightings of *A. wattsi* outside of the Waterloo area.

An additional survey was made in April to August 2004. Previous locations of *A. wattsi* and areas further afield were visited by vehicle, and single street blocks were examined on foot — these are termed sites, grouped into localities corresponding with place names. Exact locations were obtained using a Garmin GPS II Plus or a Garmin 12 XL GPS unit. All individuals of *A. wattsi* and *A. aeneus* were recorded, and their perch heights and diameters measured with a steel tape rule. The substrates on which the lizards were observed were recorded as one of 20 categories, later condensed to six: ground (including ground cover such as cut branches, bricks, and trash); walls; fences; posts (including posts in wire fences and freestanding posts); bushes (including non-woody plants); trees.

GPS locations were superimposed on layers showing roads and urban areas using the Idrisi 32 GIS program. Statistical analysis was with MINITAB, using nonparametric statistics adjusted for ties where appropriate. Each individual lizard was used only once in any analysis. Niche breadth (B) and overlap (O) were calculated after Pianka (1973):

$$B = 1/\Sigma p_i^2$$

where i is the resource category, and p_i is the proportion in category i, with summation over the total number of categories in that niche dimension.

$$O_{jk} = O_{kj} = (\Sigma p_{ij} p_{ik})/\sqrt{(\Sigma p_{ij}^2 \Sigma p_{ik}^2)}$$

where j and k are species classes. Breadth and overlap are sensitive to the number of categories, so these were calculated both for the total number of categories, and for data standardized by collapsing to six categories in each case (e.g. Howard and Hailey, 1999), as described in the results.

Results

Identification and importation

Ten specimens of *A. wattsi* from Trinidad were deposited in the Chicago Field Museum, and were confirmed as *A. wattsi wattsi* by G. Mayer, University of Wisconsin-Parkside. We therefore treat the species as *A. wattsi* in the strict sense, differentiated from sibling species (other former subspecies).

Caroni (1975) Limited's pineapple cultivation occurred at Orange Grove, about 20 km N.E. of Waterloo. Interviews with relevant employees and company correspondence suggested that the pineapple fields were established in 1986 with plant material from Tableland in south Trinidad. Pineapple plants subsequently imported in 1991 by the research station were tissue culture plantlets and not a likely route of introduction, unless on packaging material. Pineapple is no longer cultivated at Orange Grove, and no *A. wattsi* could be located at the adjacent housing compound (although three *A. aeneus* were observed there).

Documented imports with an overall score of 0.5 or greater for being a likely source of introduction of *A. wattsi* are shown in table 1. There were 21 such importations, showing the high level of agricultural and horticultural trade among Caribbean islands, presumably responsible for the large number of introduced *Anolis* populations. None of these documented cases, however, stands out as being the likely source of *A. wattsi*, so that narrowing the time of introduction into Trinidad is not possible.

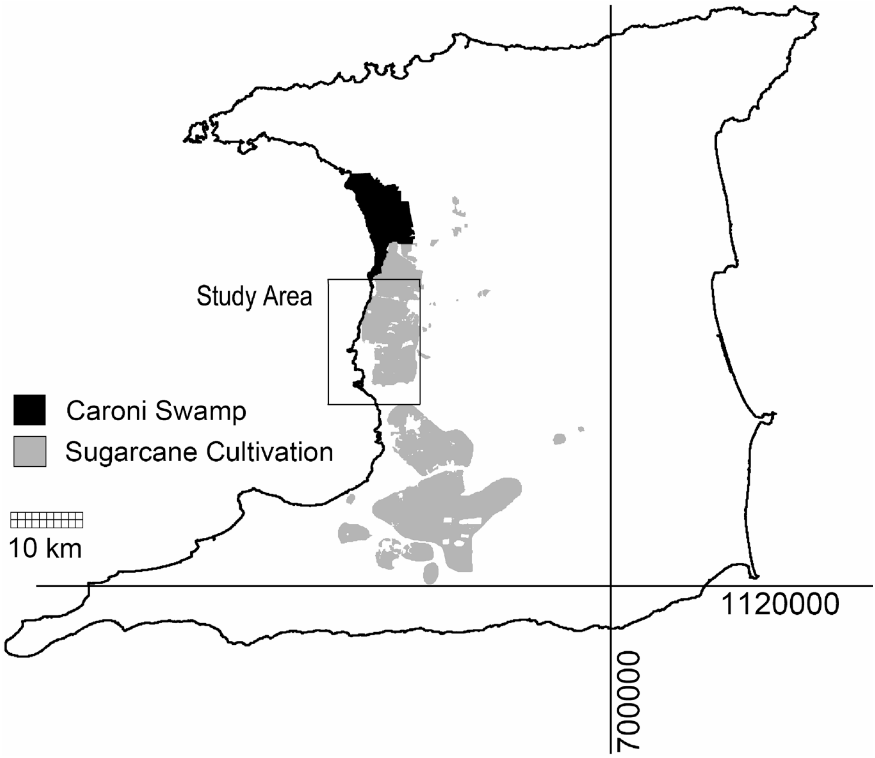

Figure 1. Location of the study area in west central Trinidad. The area occupies part of the main sugar cane growing region to the south of the Caroni Swamp, a tidal brackish swamp dominated by mangrove forest.

Distribution and spreading

The localities in which *A. wattsi* were found in 2000 were Brickfield, Waterloo, Orange Valley, Union Village and St Andrews. Except for the first two, these localities were all separated by areas of sugar cane, apparently unsuitable habitat in which no *Anolis* lizards were seen in fields or along roadsides.

A total of 70 *A. wattsi* were recorded, compared to 92 *A. aeneus*. The highest counts of *A. wattsi* were in the immediate vicinity of the Caroni Research Station (table 2 — Waterloo staff housing, Brickfield, Butler Village), with lower numbers further away (Orange Valley, Union Village, St. Andrews). *A. wattsi* had not spread to Carapichaima (contiguous with and to the east of Butler Village) or to any of the localities further from the research station (not shown), although the presence of *A. aeneus* showed that there were habitats suitable for *Anolis* lizards.

Table 2 shows an inverse relationship between numbers of the two species among the eight sites; rank correlation, $r_s = -0.719$, $P = 0.045$. This may, however, have been an artifact of the survey method, which was focused on the presence of *A. wattsi* rather than the interaction of the two species. Greater survey effort

Table 1. Import permits approved by the Trinidad and Tobago Plant Quarantine Service for the importation of plants or products, with highest likelihood of introduction of *Anolis wattsi.*

Year	County of Origin	Items	Quantity
1977	St Lucia	Ornamentals	50 Plants
1978	St Lucia	Banana Plants	100 000 Plants
1983	Antigua	Orchids	50 Plants
	St Lucia	Orchids	24 Plants
	St Lucia	Ornamentals	124 Plants
1984	Antigua	Grass	5 kg sample
	Antigua	Vegetable flower seeds	21 kg
1985	Antigua	Ornamentals	125 Plants
1986	Antigua/Barbados	Grass samples	125 kg
	Antigua	Vegetable and flower seeds	9 kg
	St Lucia/ St. Vincent	Tobacco	96 000 kg
1987	Antigua	Grass cuttings	25 kg 400 Pieces
	Antigua	Peanuts	2500 kg
1988	Antigua	Grass cuttings	15 kg
	St Lucia	Tobacco	25 000 kg
	St Lucia	Ornamentals	4500 Plants
1989	Antigua	Grass and legume seeds	Not Indicated
	Antigua	Grass seeds	Not indicated
1991	Antigua	Pineapple plants	Not indicated
	St Lucia	Pineapple plants	Not indicated
	St Lucia	Ornamentals	Not indicated

Table 2. Number of individuals of *Anolis wattsi* and A. *aeneus* observed in Waterloo and surrounding villages, July 2000.

Village	*Anolis wattsi*	*Anolis aeneus*
Adjoining Caroni Research Station	9	2
Waterloo staff housing	16	4
Butler Village	22	5
Brickfield	13	5
Carapichaima	0	13
Orange Valley	1	20
Union Village	4	31
St Andrews	5	12

was thus made in areas with very few or no *A. wattsi*, and all microhabitats were examined carefully in those areas, potentially generating large numbers of sightings of *A. aeneus*. In other areas where *A. wattsi* were abundant, most attention was paid to their frequented microhabitats such as the base of fences and drains, and it is likely that some *A. aeneus* were missed at such sites.

38 sites at 11 localities were sampled in 2004, all of which had *A. aeneus* except for one at Brickfield (*A. wattsi* only) and another at St Andrews Village (no *Anolis*). *A. wattsi* was found to have spread to Couva and California, with an outlying population at Claxton Bay (fig. 2). The Claxton Bay population was first noticed in

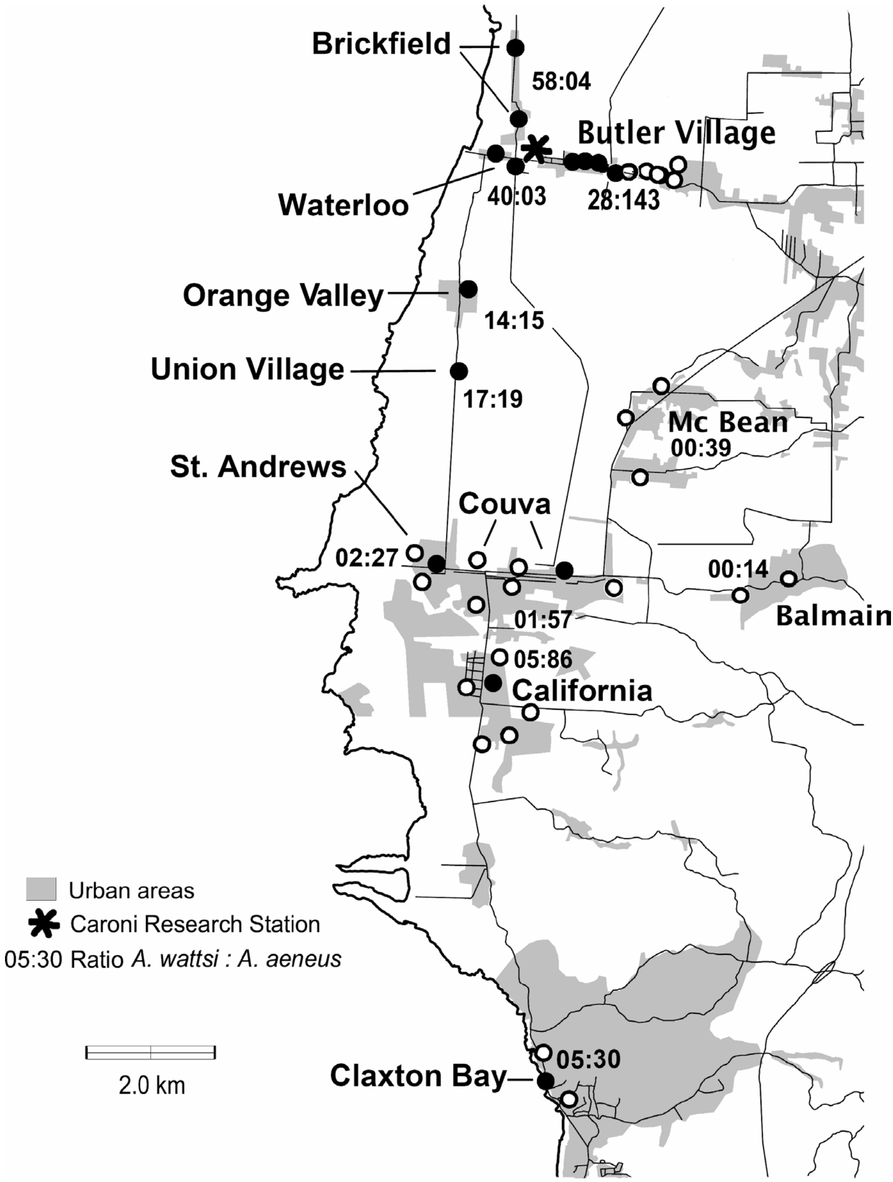

Figure 2. Survey sites with (•) or without (o) *A. wattsi*, in relation to roads and urban areas.

August 2003 by D. Baldeo (personal communication), who subsequently recognised the photograph on the cover of Living World. (There were no other reports of *A. wattsi* as a result of this request for information.) He had frequented the area for some time previously and suspected that they were a recent introduction to the site. No *A. wattsi* were observed at two sites with suitable habitats adjacent to Claxton Bay (fig. 2). There was no significant correlation between numbers of the two species among the 11 localities sampled in 2004 (data in fig. 2), when surveying was directed at both species rather than being focused on *A. wattsi*; $r_s = -0.329$, $P = 0.32$. A similar result was obtained for the 38 separate sites; $r_s = -0.230$, $P = 0.16$.

Spreading of *A. wattsi* from the Caroni Research Station was possibly linear north through Waterloo to Brickfield, and east through Butler Village, both directions with continuous urban development. *A. wattsi* had spread about 1.5 km to the northern end of Brickfield, where urban development ended at the southern border of the Caroni Swamp. *A. wattsi* had reached the north of Brickfield by 2000. The village itself had also spread northward over that time; many of the staff of the Caroni Research Station lived in Brickfield and jump dispersal was thus likely. *A. wattsi* had also spread about 1.3 km east along the Waterloo Road to Butler Village, which is contiguous with Carapichaima to the east where only *A. aeneus* was found (fig. 2). The easternmost record of *A. wattsi* was at GPS location 669166-1158606 on 31 August 2004, from where the exact rate of spread may be monitored in future. The easternmost *A. wattsi* in July 2000 was at 668546-1158728, about 620 m west of the 2004 limit.

The colonization of Butler Village gives an opportunity to estimate the maximum rate of spread of *A. wattsi* into habitat already occupied by *A. aeneus*, assuming that this was by linear dispersal rather than from a secondary centre arrived at by jump dispersal. The maximum rate would be produced by assuming that *A. wattsi* had been introduced shortly before it was observed in 1992; for example in 1991, allowing only one year for the population to reach noticeable size. This would be a spread of 1.3 km in 13 years, or 100 m yr^{-1}. A similar rate of spread (about 150 m yr^{-1}) is represented by the July 2000 and August 2004 locations.

Spreading to other localities (Orange Valley, Union Village, St Andrews / Couva / California, and Claxton Bay) was across areas of unsuitable habitat, mostly sugar cane fields, where no *Anolis* lizards were observed. Colonization of these areas represents a much higher rate of spread than to Brickfield and Butler Village. Claxton Bay is about 14.5 km from the Caroni Research Station, giving a rate of spread calculated as above of about 1.2 km yr^{-1}, an order of magnitude greater than that for linear dispersal through continuous urban areas. The high rate of spread and the unsuitable nature of the intervening areas both suggest that this was by jump dispersal, in human transport of plants or building materials. The isolated sites with *A. wattsi* within the St Andrews / Couva / California complex, and the failure to reach McBean and Balmain, also suggest a pattern of jump dispersal.

Interaction with A. aeneus

Perch heights were not normally distributed, and tended to be lower in *A. wattsi* than *A. aeneus* (fig. 3). This difference was significant (table 3; Mann-Whitney test, $P < 0.0001$). The possible effect of competition with *A. wattsi* on perch height in *A. aeneus* was examined by separating these data into three categories: 1. *A. aeneus* close to *A. wattsi*, defined as records being two minutes or less apart.

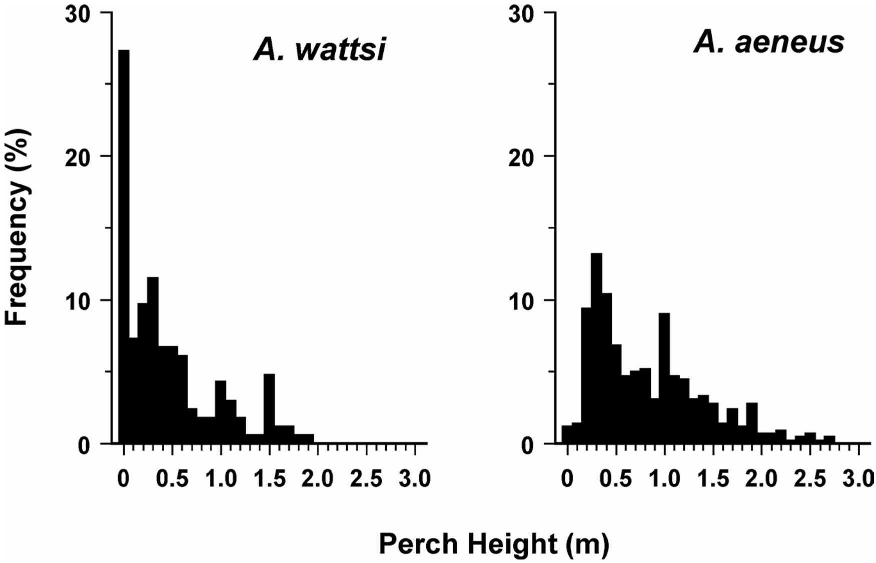

Figure 3. Perch heights of *Anolis wattsi* and *A. aeneus* in west-central Trinidad.

Table 3. Perch characteristics of *Anolis wattsi* and *A. aeneus* in west-central Trinidad. Values are mean ± SD (with number of individuals).

Perch characteristic	*A. wattsi*	*A. aeneus*
Height (m)	0.46 ± 0.49 (165)	0.83 ± 0.58 (424)
close to *A. wattsi*	–	0.86 ± 0.53 (63)
not near *A. wattsi*	–	0.92 ± 0.55 (70)
without *A. wattsi*	–	0.81 ± 0.59 (291)
Diameter (cm)	11 ± 15 (59)	12 ± 13 (297)

2. *A. aeneus* at sites with *A. wattsi* but not close, defined as being recorded three or more minutes from the nearest *A. wattsi*. 3. *A. aeneus* at sites without *A. wattsi*. There was no difference between perch heights of *A. aeneus* in the three situations (table 3; Kruskal-Wallis test, $H = 4.44$, 2 df, $P = 0.109$).

Perch diameter was similar in *A. wattsi* and *A. aeneus* (fig. 4), and did not differ significantly between the two species (table 3; Mann-Whitney test, $P = 0.28$), or among *A. aeneus* in the three situations with respect to proximity of *A. wattsi* (Kruskal-Wallis test, $H = 3.35$, 2 df, $P = 0.187$).

There was a significant difference in substrate used by the two species (table 4; $\chi^2 = 141, 5$ df, $P < 0.001$). *A. wattsi* was prevalent on the ground, and *A. aeneus* was prevalent on trees (table 4). The balance between the two species shifted in the sequence ground (87% of *Anolis* being *wattsi*), walls and fences (approximately 30% *wattsi*), posts and bushes (approximately 20% *wattsi*), and trees (only 6% of *Anolis* being *wattsi*).

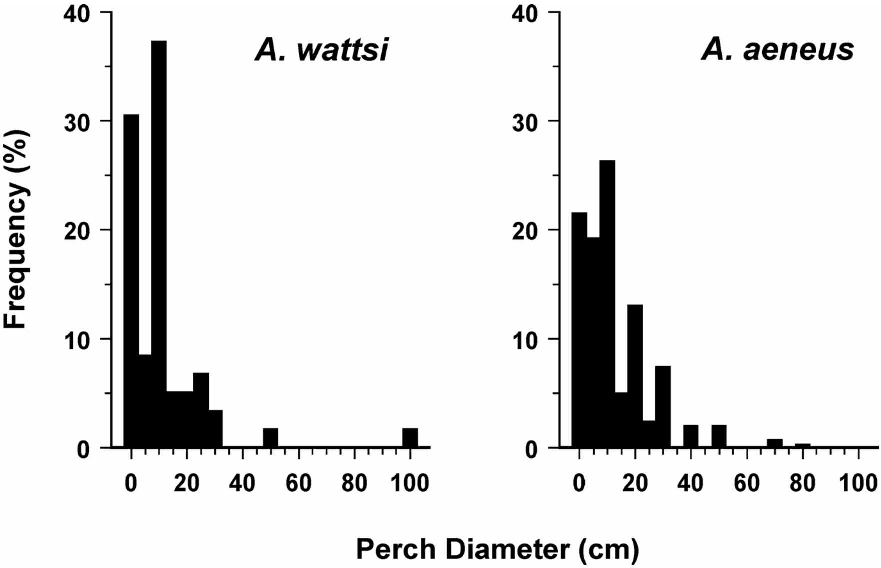

Figure 4. Perch diameters of *Anolis wattsi* and *A. aeneus* in west-central Trinidad. (The 1.0 m diameter perch was a short cycad.)

Table 4. Substrates used by *A. wattsi* and *A. aeneus* in west-central Trinidad. Values are proportions of the total for each species (p_i), with the percentages of the total *Anolis* observed on each substrate in parentheses, and total sample sizes (n).

Substrate	*A. wattsi*	*A. aeneus*	*n*
Ground	0.33 (87)	0.02 (13)	63
Wall	0.25 (28)	0.25 (72)	146
Fence	0.12 (30)	0.10 (70)	63
Post	0.16 (21)	0.23 (79)	122
Bush	0.11 (19)	0.18 (81)	94
Tree	0.04 (6)	0.22 (94)	101
n	165	424	589

Niche breadth was generally greater in *A. aeneus* than in *A. wattsi* (table 5), for all three dimensions (substrate, perch height and diameter) for both methods of calculation. Values of breadth and overlap were standardized to 6 categories for comparability between niche dimensions, using: the substrate categories shown in table 4; categories of perch height formed from four adjacent bins of those shown in fig. 3; categories of perch diameter formed from two adjacent bins of those shown in fig. 4. Overlap was high for perch diameter ($O = 0.98$), as expected since the distributions for the two species were not significantly different. There was lower overlap for perch height ($O = 0.84$), where the distributions for the two species were significantly different. Niche breadth for perch height was much lower for *A. wattsi* ($B = 2.7$) than for *A. aeneus* ($B = 4.7$), reflecting the dominance of the zero height bin for *A. wattsi* (fig. 3). There was even lower overlap for substrate type

Table 5. Niche breadth and overlap for *A. wattsi* and *A. aeneus* in west-central Trinidad. These have been calculated for the categories originally recorded, and standardized to six categories for each niche dimension.

Niche dimension	No. of categories	Breadth *A. wattsi*	Breadth *A. aeneus*	Overlap
Substrate	20	7.84	11.42	0.636
Perch height	14	5.00	7.73	0.669
Perch diameter	12	3.98	5.59	0.914
Substrate	6	4.46	4.85	0.666
Perch height	6	2.65	4.74	0.839
Perch diameter	6	2.87	3.39	0.979

($O = 0.67$) reflecting the preponderance of *A. wattsi* on the ground and *A. aeneus* on trees. These patterns suggest that use of the ground was the major difference between the two species, and that this represents a separate category of the niche, rather than merely a value of zero along a continuum of perch height.

Discussion

Establishment of A. wattsi *in Trinidad*

It is clear that *A. wattsi* has become well established in west central Trinidad, from an initial introduction in the Waterloo area. The species has now been present for at least 12 years, and can be described as naturalized. The population must already number thousands, if not tens of thousands, and has obviously overcome the likely problems of a genetic bottleneck (Gorman et al., 1978). No direct evidence was gained that the introduction was on pineapple plants, or even that this was from Antigua; while some pineapple plants were imported this was either tissue culture material or did not reach Caroni Research Station. The source and timing of introduction therefore remain unresolved.

Two patterns of spreading were observed; at a rate of perhaps 100 m yr^{-1} through continuous urban areas, and at a rate an order of magnitude higher across intervening areas of unsuitable sugar cane habitat. The large areas of monoculture, use of chemical pesticides, and annual burning of the crop contribute to the difficulty of spreading through sugar cane, but *A. wattsi* has successfully overcome several such barriers. The rate of spreading by jump dispersal is, of course, limited by human rather than lizard movements, and so much greater spreading of *A. wattsi* through Trinidad may be expected, with outlying populations possible anywhere in the country.

Anolis lizards have small home ranges, of the order of 20 m^2 or less (Gorman and Harwood, 1977), and it is likely that linear spreading through continuous urban areas is by dispersal of juveniles. The estimated rate of spread of about 100 m yr^{-1} is feasible for *Anolis* lizards. Andrews and Rand (1983) recorded home ranges of individual *A. limifrons* observed as both juveniles and adults to be separated by up to 30-40 m.

Interaction with A. aeneus

Anolis wattsi has become established in Trinidad despite the presence of *A. aeneus* in the same area and habitat. There are six possible outcomes of the interaction between these species: 1. Failure of *A. wattsi* to become established; 2. coexistence with complete habitat separation; 3. hybridization; 4. coexistence in the same habitat with competition; 5. coexistence in the same habitat without competition; 6. replacement of *A. aeneus* by *A. wattsi*. The present study shows that the first two possibilities can be rejected; *A. wattsi* has become established, and in the same habitat as *A. aeneus*. Negative interactions due to hybridization are also unlikely. *A. aeneus* does hybridize with *A. trinitatis* (Gorman, 1969; Gorman and Yang, 1975), and the resulting offspring show poor reproductive potential (Gorman et al., 1971). Gorman and Yang (1975) concluded that *A. aeneus* may force *A. trinitatis* to extinction in Trinidad due in part to this hybridization. These two species are members of the southern Antillean *roquet* group of *Anolis* (Giannasi et al., 2000); interbreeding with *A. wattsi*, of the northern Antillean *bimaculatus* group (Gorman and Kim, 1976), is less likely. In the southern Antillean island of St Lucia, where *A. wattsi* has also been introduced, it does not appear to be hybridizing with the native species *A. luciae* (Giannasi et al., 1997).

The remaining possible outcomes involve coexistence within the same habitats, as observed, with and without interspecific competition, or eventual replacement of *A. aeneus* by *A. wattsi*. There were differences between the niches of the two species, with *A. wattsi* being more terrestrial and using lower perches than *A. aeneus*, but it remains an open question whether these differences (or others) are sufficient to avoid competition. Perch height is largely a reflection of body size in anoles — large species use higher perches to give larger search areas for larger prey, but body size is the primary means of niche separation (Roughgarden, 1995). The important questions are thus whether *A. wattsi* is of sufficiently different body size from *A. aeneus* to avoid competition, and whether there are other likely dimensions of niche separation independent of body size.

The situations in other islands with *A. wattsi* and its sibling species are relevant to the first question. On St Eustatius, *A. schwartzi* (formerly *A. wattsi schwartzi*) coexists naturally with the larger *A. bimaculatus* (table 6) with no significant competitive effects (Pacala and Roughgarden, 1982, 1985). There was a difference in perch height between *A. schwartzi* (<0.5 m) and *A. bimaculatus* (>1.5 m), but experiments with limited perch availability showed that perch height was not itself an important dimension of niche separation (Rummel and Roughgarden, 1985). On St Maarten, *A. pogus* (formerly *A. wattsi pogus*) coexists naturally with the medium sized *A. gingivinus* (table 6). These two species show less spatial niche separation, and there are competitive effects of *A. pogus* on *A. gingivinus* (Pacala and Roughgarden, 1982, 1985). Schall (1992) also showed that these two species are

Table 6. Maximum male snout-vent lengths (mm) of *Anolis* species (on their native islands) discussed in relation to Trinidad (from Roughgarden, 1995; Murphy, 1997).

Island	Small-medium species, SVL		Medium-large species, SVL	
Grenada	*aeneus*	77	*richardii*	125
St Vincent	*trinitatis*	74	*griseus*	127
Antigua	*wattsi*	58	*leachii*	111
St Eustatius	*schwartzi*	49	*bimaculatus*	90
St Maarten	*pogus*	50	*gingivinus*	72
Trinidad	*chrysolepis*	68		
Barbados	*extremus*	83		
St Lucia	*luciae*	91		

competitors. *A. wattsi* has become abundant in St Lucia, where the native *A. luciae* is a medium sized species (table 6), while the other naturalized species, the medium sized *A. extremus*, remains uncommon (Gorman, 1976).

These studies suggest that, without separation along other niche dimensions, a difference in body size of about 40-50 mm is needed to avoid interspecific competition, and has evolved in natural two-species islands (table 6; Grenada, St Vincent, Antigua, St Eustatius). A smaller difference of 22 mm allows coexistence but with significant competition between *A. pogus* and *A. gingivinus* on St Maarten. The difference in body size of about 20 mm between *A. wattsi* and *A. aeneus* thus suggests that there should be competition between these two species unless other niche dimensions are involved.

A possible indication of interspecific competition is that *A. wattsi* was much more abundant than *A. aeneus* in Brickfield and Waterloo (fig. 2), suggesting that *A. wattsi* was replacing the earlier naturalized species. If taken to completion, this would be the sixth possible outcome of the interaction between the two species. Nevertheless, the perch height of *A. aeneus* was not affected by the presence or absence of *A. wattsi*, and there was no general negative relationship between numbers of the two species among sites. These latter patterns suggest a lack of competition, and thus that another niche dimension was also involved. The most likely such dimension would be substrate type, with the ground being a separate category rather than merely a zero perch height. The curved raised "scorpion tail" of *A. wattsi* may for example represent an adaptation to a ground-living niche. One possibility requiring further research is that Brickfield and Waterloo were less suitable for *A. aeneus*, for example with less walls and trees, so that the larger numbers of *A. wattsi* there were not the result of competitive displacement.

Interactions among Anolis *species in Trinidad*

It is likely that *A. wattsi* and *A. aeneus* will be able to coexist in the same habitats in Trinidad, in contrast to the more similarly sized *A. aeneus, A. extremus* and *A. trinitatis* (A. Hailey, V.C. Quesnel and H.E.A. Boos, in preparation). Introduced *Anolis* in Trinidad have not penetrated into undisturbed areas, in common with most other naturalized herpetofauna (Lever, 2003). If it does so, *A. wattsi* is more likely to compete with the native *A. chrysolepis* than are other introduced species in view of the ground-dwelling habits of the latter (Murphy, 1997).

The addition of *A. wattsi* to the herpetofauna of Trinidad leads to the question of how many *Anolis* species might be expected to survive there. Comparably sized Antillean islands have larger numbers of native species: Jamaica 7 (plus introduced species; Haefner, 1988), Puerto Rico 11, Hispaniola and Cuba more than 35 species each (Roughgarden, 1995). Trinidad, however, as a land-bridge island has a largely continental fauna, including birds which compete with and prey upon lizards and limit their population density (Andrews, 1976). There are also other tree-dwelling lizards in Trinidad, which all utilize parts of a potential anole niche: *Polychrus marmoratus*, *Tropidurus plica* and *Mabuya bistriata*.

A large species such as *A. richardii* (table 6) would seem the most likely candidate for successful addition to the *Anolis* fauna of Trinidad. This species coexists with *A. aeneus* in its native Grenada (Schoener and Gorman, 1968), and is already naturalized in Tobago where it is the only anole present (Murphy, 1997). The other naturalized species in Trinidad also coexist with larger species in their native islands; *A. trinitatis* with *A. griseus* in St. Vincent, and *A. wattsi* with *A. leachii* in Antigua (table 6). It is thus likely that the *Anolis* fauna of Trinidad is not yet saturated, and further successful introductions can be anticipated.

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