

# Interspecific competition among urban cockroach species

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## Abstract

The aim of this study was to quantify and to compare the effects of intraspecific and interspecific competition among pairs of urban cockroaches [*Blatta orientalis* L., *Periplaneta americana* (L.), and *Periplaneta australasiae* Fabricius (Dictyoptera: Blattodea)] in relation to the limitation of resources such as shelter or food. Our approach was to assess whether the presence of one species affected the resource exploitation of another. A reduction in access to shelters or to food for one species revealed dominant/subordination relationships among species and induced spatial segregation in shelters and temporal segregation during food exploitation. The fragmentation of available resources facilitated spatial segregation and the access of more individuals of the subordinate species. Individuals of each species were aware of the presence of non-conspecifics. The outcome of interspecific competition under laboratory conditions should help us to understand how segregated spatial distributions occur under natural conditions in urban areas.

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## Introduction

Interspecific competition plays an important role in shaping communities by determining which and how many species coexist. Interspecific competition occurs when several species depend on a resource that is insufficient for all, and can lead to the exclusion of the inferior competitor species or to an unbalanced sharing of resources (Hardin, 1960). For example, invasive Argentine ants dominate native ant species by preying on them and by exploiting the same food resources (Human & Gordon, 1996). An unbalanced sharing of resources is observed when the presence of one species of earthworms reduces the burrowing of another earthworm species (Capowiez, 2000). The coexistence of competing species can be facilitated by a temporal shift of activity, as was observed in niche partitioning among four ant species (Albrecht & Gotelli, 2001). In addition, spatial segregation due to the fragmented distribution of resources increases species coexistence. The coexistence of two fly species can be obtained by increasing patch fragmentation, although one species is always eliminated in a non-fragmented habitat (Pimentel et al., 1965; Ayala, 1969). The ability of a species to invade and to maintain

itself in an environment depends on its interactions with other species competing for the same resources.

Some cockroach species are able to settle in urban habitats that provide all the required resources and environmental conditions (food, water, harbourage, temperature, and moisture) (Cornwell, 1968). Urban species share a large variety of ecological requirements and of life history traits, among which gregariousness, nocturnal activity, and omnivorous diets are the most important (Cornwell, 1968; Bell & Adiyodi, 1981; Rivault, 1989, 1990; Brenner et al., 1998). The distribution of urban cockroach species has mainly been documented through the outcome of insecticide treatments. Pest control operators usually report the presence of only one species in one building (Cornwell, 1968; Wildey & Robinson, 1993; Rust et al., 1995; Wildey, 1996; Robinson et al., 1999). Mixed populations, such as a mixed population of *Periplaneta americana* and *Periplaneta australasiae* observed in Australia, have rarely been mentioned (Miller & Peters, 2002). More than 10 years of campaigns of insecticide cockroach control in France have revealed a mosaic distribution of species within each prospected town, but no species overlap at flat or building levels. No more than one species was observed in a given building, although the buildings had identical use, state, and microclimatic conditions (Rivault, 1991; Cloarec et al., 1999). As no differences in environmental variables can explain

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which species occupies a building, and why only one species occupies that building, we hypothesized that interspecific competition for space and food would influence the distribution of urban cockroach species.

Our aim was to quantify and to compare the effects of intra- and interspecific competition among three urban cockroaches [*Blatta orientalis* L., *Periplaneta americana* (L.), and *Periplaneta australasiae* Fabricius (Dictyoptera: Blattodea)] in relation to the limitation of resources such as shelter or food. An experimental approach assessed whether the presence of one species affected resource exploitation by another. Distance to nearest neighbour was used to evaluate aggregation levels and distribution, in relation to species, inside the shelters. The outcome of interspecific competition under laboratory conditions should help our understanding of how segregated spatial distributions occur under natural conditions in urban areas.

## Materials and methods

### Biological material and experimental set-up

Three similar sized cockroach species with largely overlapping distribution areas in urban habitats were studied: *Blatta orientalis* L., *Periplaneta americana* (L.), and *Periplaneta australasiae* Fabricius. All belong to the family Blattidae of the order Dictyoptera (Cornwell, 1968). These three species are nocturnal, and their activity peaks during the first hours of the night (Rivault, 1985). Stock cultures were maintained in cages at 25 °C under a L12:D12 photoperiod. Commercial dog pellets (1 cm in diameter) and water were provided ad libitum. Only adults that had moulted less than 10 days before, and last instar larvae were selected for experiments, thus minimizing any age and body size effects.

The experimental conditions (temperature and photoperiod) were the same as the breeding conditions. The shelter experiments were carried out in glass arenas (60 × 60 × 40 cm). Cardboard shelters (10 × 8 × 2 cm) were fixed on to the inner side of a wall. Pieces of cardboard, fixed on the outside wall, darkened the shelters and could be lifted to observe cockroaches in the shelters without disturbing them. Food competition was investigated by introducing a single small food source into the arena after the cockroaches had fasted there for 4 days. One dog pellet, in a plastic Petri dish, was introduced just after nightfall, in the middle of the arena. Its size was such that no more than eight of the 20 subjects had simultaneous access to it. Water was provided ad libitum.

### Protocol and data collecting

*Shelter occupancy.* Shelter occupancy by all the cockroaches in each group was estimated by direct observation of

their positions, either in or out of the dark shelter, during the light period when they were generally resting, and immobile. Preliminary experiments tested the experimental set-up and species differences. Groups of 20 cockroaches of each species were allowed to settle in the arena for 2 days; they were called 'residents'. The sizes of the shelters were evaluated so that they housed all the residents. In this case, residents of all species preferred to rest in shelters rather than to stay outside (binomial test,  $P < 0.0001$ , in all cases). Although the shelters were attractive resting places for all species, the proportions of individuals housed in the shelters varied significantly with species (ANOVA;  $F_{2,53} = 36.9$ ,  $P < 0.0001$ ) (proportions of sheltered individuals in groups of 20 residents: *B. orientalis*: 86%; *P. americana*: 78%; *P. australasiae*: 55%). On the third day, a second group of 20 cockroaches was added, thus increasing the population density. These added cockroaches were called 'intruders'. Residents were distinguished from intruders by a dot of white paint on their pronotum. We tested resident effect and species effect by comparing four treatments for each pair tested. Each species was tested as resident as well as intruder, in intra- as well as in interspecific encounters. Encounters occurred between two groups of 20 individuals of each species. As *P. americana* shared several ecological requirements with the two other species, we chose to pair *P. americana* with *P. australasiae* and *P. americana* with *B. orientalis*. Numbers of replicates for each treatment are detailed in Table 1. All individuals were only tested once.

The positions of all the cockroaches inside the shelters were noted on a grid and then transformed into X–Y co-ordinates. The position of the head was chosen as the reference point for each individual. Co-ordinates for each individual were used to calculate distances to their nearest neighbour (Clark & Evans, 1954). Two types of nearest neighbour were considered: (a) during intraspecific encounters, distance to nearest resident neighbour and distance to nearest intruder neighbour; and (b) during interspecific encounters, distance to nearest intraspecific neighbour and distance to nearest interspecific neighbour (Figure 1).

*Access to food.* The cockroaches were observed for 2 h under a red light during the first 2 h of the dark phase to evaluate access to food sources by different groups. Twenty scans per arena were recorded regularly, at 6 min intervals, to evaluate the number of cockroaches feeding. Feeding activity was evaluated by the mean proportions of individuals feeding on the food source per scan. Co-occurrence of both species was evaluated by the proportions of scans recording at least one cockroach of each species together simultaneously on one food source in relation to the total number of scans recording the presence of at least two cockroaches on one food source. Group compositions for *P. americana*–

**Table 1** Shelter occupancy and food access: numbers of replicates for intraspecific and interspecific encounters

		One shelter	Two shelters			One food source	Two food sources
Intraspecific encounters	<i>B. o.</i> –( <i>B. o.</i> )	20	20	<i>B. o.</i> – <i>B. o.</i>		18	26
	<i>P. am.</i> –( <i>P. am.</i> )	20	20	<i>P. am.</i> – <i>P. am.</i>		18	26
	<i>P. aus.</i> –( <i>P. aus.</i> )	16	15	<i>P. aus.</i> – <i>P. aus.</i>		16	
Interspecific encounters	<i>B. o.</i> –( <i>P. am.</i> )	20	20				
	<i>P. am.</i> –( <i>B. o.</i> )	20	20	<i>B. o.</i> – <i>P. am.</i>		20	22
	<i>P. am.</i> –( <i>P. aus.</i> )	15	15	<i>P. aus.</i> – <i>P. am.</i>		16	
	<i>P. aus.</i> –( <i>P. am.</i> )	16	15				

*P. am.*: *Periplaneta americana*; *B. o.*: *Blatta orientalis*; *P. aus.*: *Periplaneta australasiae*. Names of intruder groups in shelter occupancy experiments are indicated in brackets.

*P. australasiae* and for *P. americana*–*B. orientalis* encounters were the same as those in the shelter occupancy tests. Numbers of replicates for each type of encounter are detailed in Table 1.

*Unlimited access to resources.* To evaluate the effect of resource availability, either two identical shelters or two identical food sources were placed in the arenas. Thus shelters or food access were no longer the limiting factors. Because of stock culture limitation, *P. australasiae* was not tested in the unlimited food source experiments. Numbers of replicates for each type of intraspecific and interspecific encounter are detailed in Table 1.

*Data analyses.* Student t-tests and ANOVAs, computed with Statview software (1998), were used to evaluate variations in shelter occupancy, access to food sources, and distances to nearest neighbours. Data were arcsine transformed

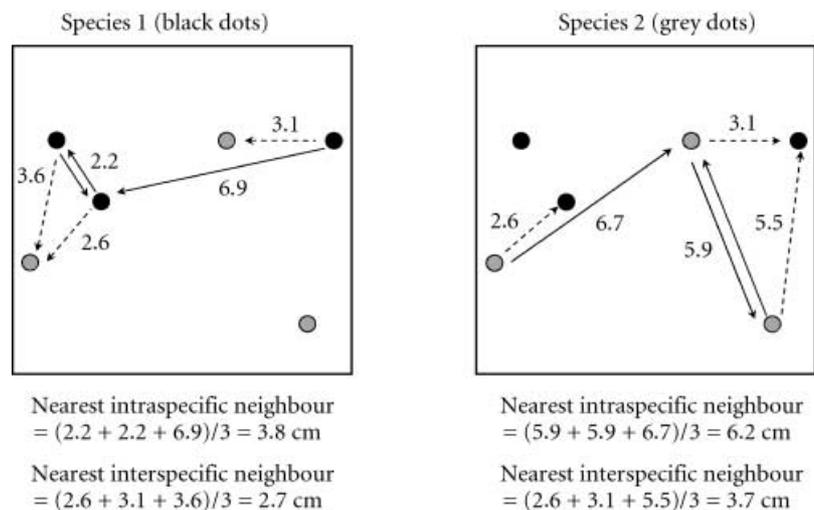
before proportions of cockroaches were compared using parametric tests (Sokal & Rohlf, 1981).

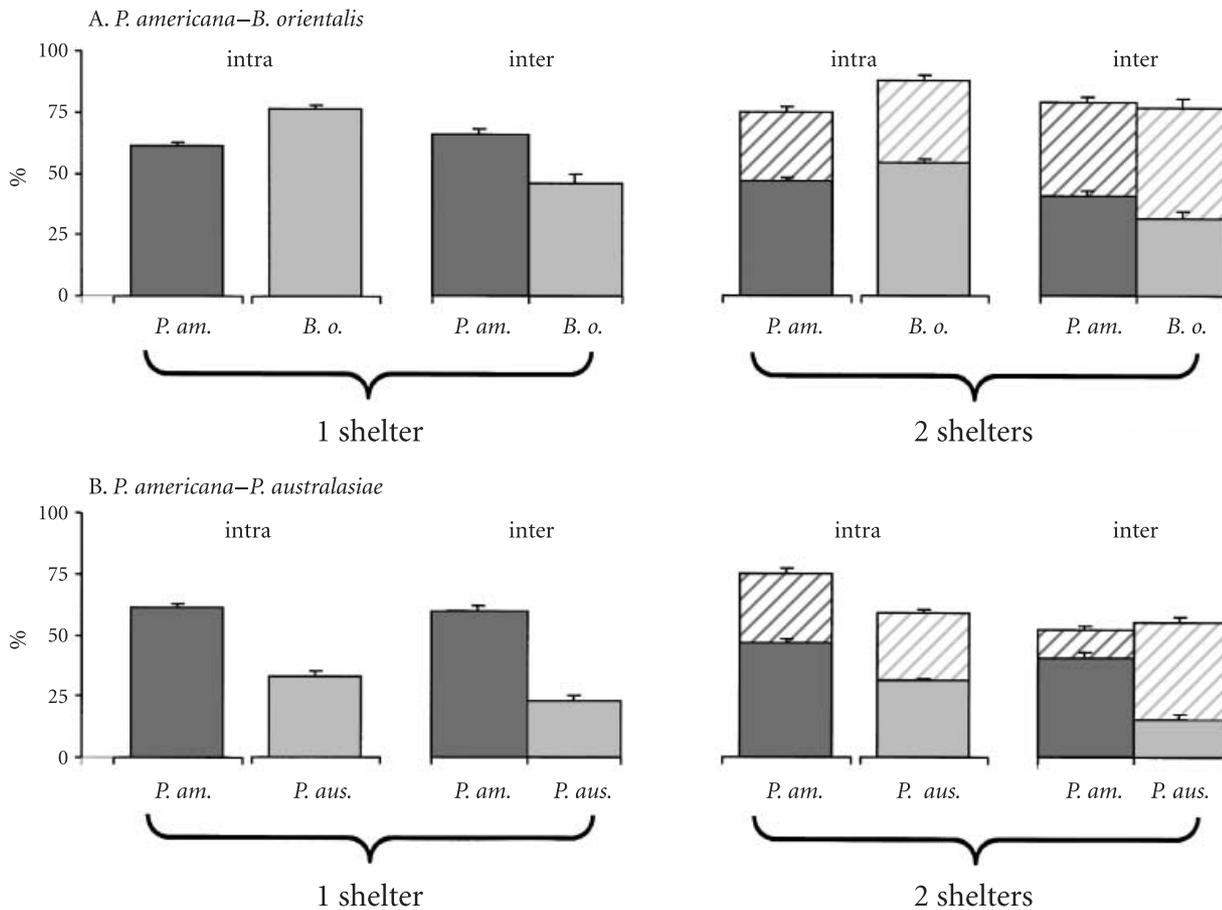
## Results

### Intraspecific experiments

*Shelter occupancy.* After the addition of an intruder group, which doubled the initial density in the arena, the total numbers of cockroaches present in the shelter increased, but the proportions of sheltered individuals were significantly lower than when the residents of any all the three species were alone (ANOVA;  $F_{1,106} = 90.1$ ,  $P < 0.0001$ ). When population densities increased, the shelters became too small to house all the cockroaches. We tested whether the residents had an advantage over intruders concerning their access to shelter. No significant differences were observed between the numbers of residents and the numbers of intruders present in the shelters (ANOVA;  $F_{1,106} = 0.41$ ,  $P = 0.84$ ).

**Figure 1** Calculation of distances to nearest neighbours during interspecific encounters. Two values were calculated: nearest intraspecific neighbour, and nearest interspecific neighbour. The left and right diagrams have the same distributions of individuals of both species. The left diagram indicates calculations for species 1, the right for species 2. Black dots: species 1; grey dots: species 2; solid lines indicate distances to nearest intraspecific neighbour; dotted lines: distances to nearest interspecific neighbour. The same method was used to calculate distances to nearest resident neighbour and distance to nearest intruder neighbour in intraspecific encounters.



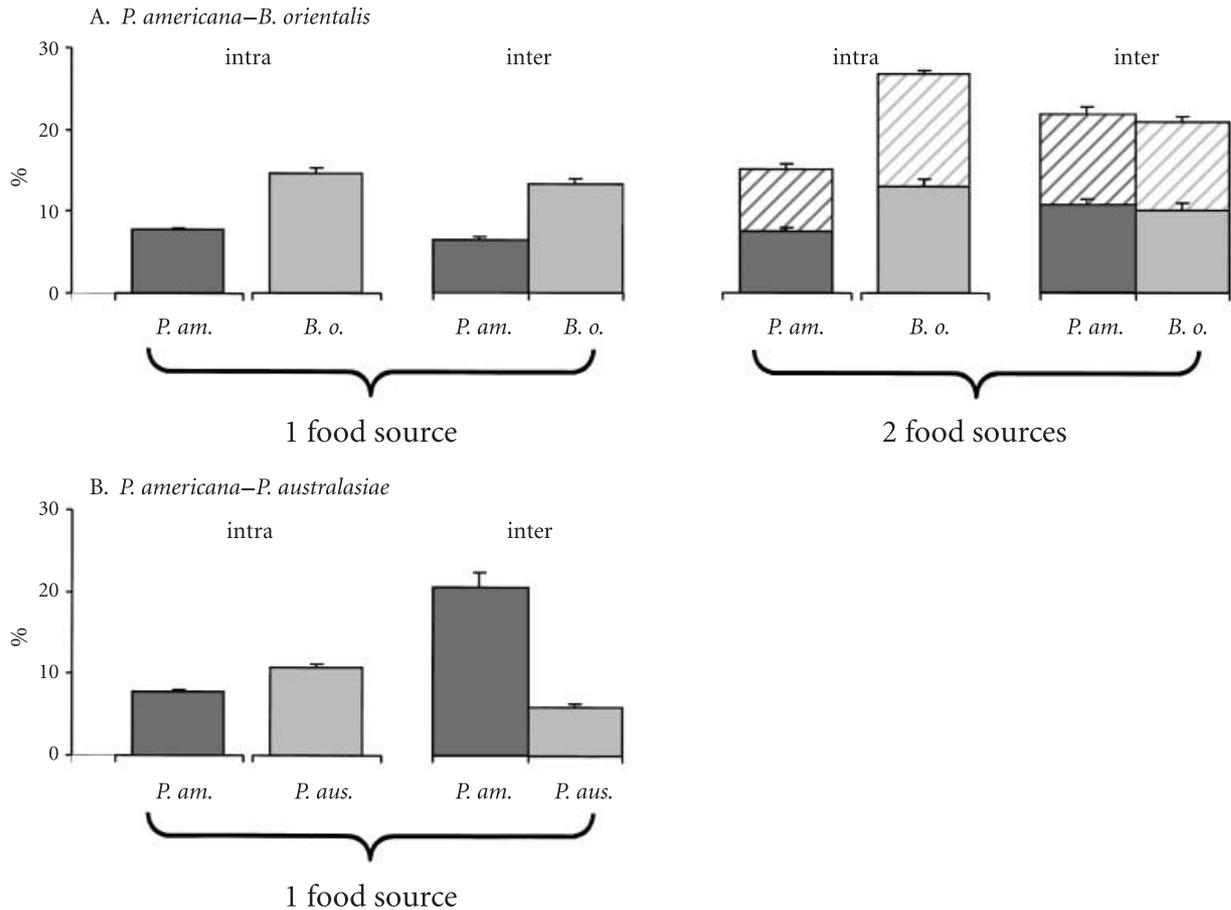


**Figure 2** Presence (mean proportions + SE) of cockroaches in shelters during intra- and interspecific encounters. (A) *P. americana*–*B. orientalis* pairs. From left to right: sheltered *P. americana* in intraspecific encounters with one shelter (dark grey bar); sheltered *B. orientalis* in intraspecific encounters with one shelter (light grey bar); sheltered cockroaches in interspecific encounters with one shelter (*P. americana*: dark grey bar, plus *B. orientalis*: light grey bar); sheltered *P. americana* in intraspecific encounters with two shelters (*P. americana* in shelter 1: dark grey bar, and *P. americana* in shelter 2: dark grey striped bar); sheltered *B. orientalis* in intraspecific encounters with two shelters (*B. orientalis* in shelter 1: light grey bar, and *B. orientalis* in shelter 2: light grey striped bar); sheltered cockroaches in interspecific encounters with two shelters (*P. americana* in shelter 1: dark grey bar and *P. americana* in shelter 2: dark grey striped bar plus *B. orientalis* in shelter 1: light grey bar, and *B. orientalis* in shelter 2: light grey striped bar). (B) *P. americana*–*P. australasiae* pairs. Same legend as above.

Furthermore, distances to nearest neighbours did not significantly differ between residents and intruders (ANOVA;  $F_{1,1802} = 0.004$ ,  $P = 0.95$ ). Thus, data for residents and intruders were pooled in subsequent analyses. A species effect was observed on the proportions of individuals housed in the shelters (ANOVA;  $F_{2,106} = 143$ ,  $P < 0.0001$ ) (Figure 2), and on the distances to nearest neighbour. Mean nearest neighbour distances were:  $1.16 \pm 0.02$  cm for *B. orientalis*,  $1.41 \pm 0.06$  cm for *P. americana*, and  $2.20 \pm 0.08$  cm for *P. australasiae* (ANOVA;  $F_{2,741} = 16.1$ ,  $P < 0.0001$ ). The greater the distance to nearest neighbour, the fewer cockroaches there were in the shelters (correlation coefficient =  $-0.95$ ,  $P < 0.05$ ). During intraspecific encounters, the intruders

gained access to the shelters as easily as the residents. Individuals of both groups mixed homogeneously inside the shelters. No asymmetry in contests and no discrimination between residents and intruders could be seen.

When two shelters were available, more cockroaches gained access to the shelters than when only one was present (ANOVA;  $F_{1,113} = 126$ ,  $P < 0.0001$ ) (Figure 2), and distances to the nearest neighbour increased significantly compared to the one-shelter experiments (ANOVA;  $F_{1,4368} = 129$ ,  $P < 0.0001$ ). These results indicated that an increase in shelter availability seemed to decrease intraspecific competition. For all species tested, an ANOVA revealed that one of the shelters always contained significantly more individuals



**Figure 3** Presence (mean proportions + SE) of cockroaches on food during intra- and interspecific encounters for each species: (A) *P. americana*–*B. orientalis* pairs. From left to right: feeding *P. americana* in intraspecific encounters with one food source (dark grey bar); feeding *B. orientalis* in intraspecific encounters with one food source (light grey bar); feeding cockroaches in interspecific encounters with one food source (*P. americana*: dark grey bar, plus *B. orientalis*: light grey bar); feeding *P. americana* in intraspecific encounters with two food sources (*P. americana* on source 1: dark grey bar and *P. americana* on source 2: dark grey striped bar); feeding *B. orientalis* in intraspecific encounters with two food sources (*B. orientalis* on source 1: light grey bar and *B. orientalis* on source 2: light grey striped bar); feeding cockroaches in interspecific encounters with two food sources (*P. americana* on source 1: dark grey bar and *P. americana* on source 2: dark grey striped bar plus *B. orientalis* on source 1: light grey bar, and *B. orientalis* on source 2: light grey striped bar). (B) *P. americana*–*P. australasiae* pairs. Intra- and interspecific encounters with one food source. Same legend as above. For full species names see Table 1.

than the other (ANOVA;  $F_{1,228} = 64.2$ ,  $P < 0.0001$ ). The distributions of the resident and intruder groups in the two shelters did not differ significantly (ANOVA;  $F_{1,228} = 1.81$ ,  $P = 0.18$ ). When the shelters were doubled and access was no longer a limiting factor, more animals were housed in the shelters, but one of the shelters attracted more individuals. This did not fit the expected equal distribution between the two shelters.

**Food access.** Duration of food intake, estimated by the proportions of cockroaches present on the food source per scan during the 2 h observations varied in relation to species: *B. orientalis* =  $0.38 \pm 0.05$ , *P. americana* =  $0.26 \pm 0.05$ , and

*P. australasiae* =  $0.32 \pm 0.05$  (ANOVA;  $F_{2,1357} = 147$ ,  $P < 0.0001$ ) (Figure 3).

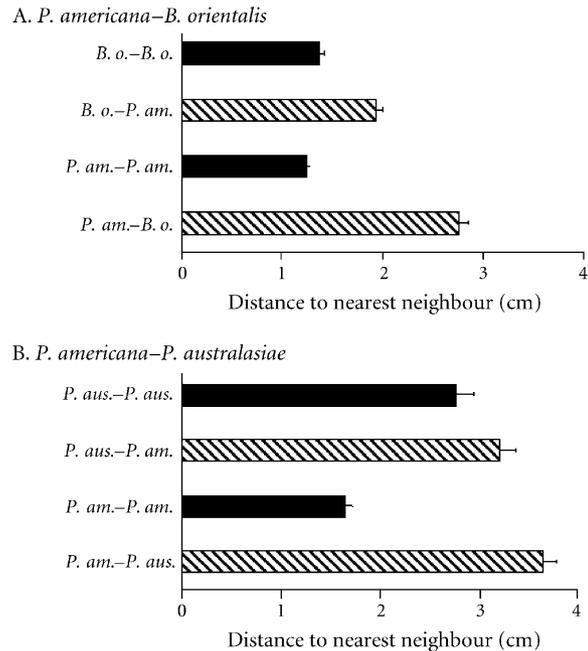
The presence of a second food source allowed a higher proportion of cockroaches to exploit food simultaneously compared to the one-food source experiments (ANOVA;  $F_{1,1756} = 366$ ,  $P < 0.0001$ ). The proportions of cockroaches present on each food source during the 2 h observations did not differ significantly between sources (ANOVA;  $F_{1,1436} = 1.15$ ,  $P = 0.283$ ). Whatever the number of available food sources, food intake was more important during the first observational hour than during the second (ANOVA;  $F_{1,4936} = 230.68$ ,  $P < 0.0001$ ). When the number of food sources was doubled, intraspecific competition for food

access decreased, and individuals were equally distributed between the two food sources (Figure 3).

#### Interspecific encounters

**Shelter occupancy.** The proportions of *P. americana* sheltered during encounters with *B. orientalis* or with *P. australasiae* did not differ significantly from the proportions of *P. americana* sheltered during intraspecific encounters (t-test; *P. americana*–*B. orientalis*:  $t = 1.77$ , d.f. = 78,  $P = 0.08$ ; *P. americana*–*P. australasiae*:  $t = -1.54$ , d.f. = 54,  $P = 0.13$ ) (Figure 2). We therefore concluded that *P. americana* did not modify their resting behaviour during encounters with either *B. orientalis* or *P. australasiae*. On the contrary, the proportions of either *B. orientalis* or *P. australasiae* sheltered were significantly lower than during intraspecific encounters (t-test; *B. orientalis*:  $t = -7.10$ , d.f. = 78,  $P < 0.0001$ ; *P. australasiae*:  $t = -4.97$ , d.f. = 46,  $P < 0.0001$ ). These results indicated that access by *P. australasiae* or by *B. orientalis* to the shelter was limited by the presence of *P. americana*. In all cases, distances to nearest intraspecific neighbour were shorter than distances to nearest interspecific neighbour (ANOVA;  $F_{1,2323} = 213$ ,  $P < 0.0001$ ) (Figure 4). Although individuals of both interacting species occupied the shelters simultaneously, inside the shelters their distributions indicated a tendency to segregate. Furthermore, the decrease in the proportions of sheltered individuals was higher for *P. australasiae* than for *B. orientalis* (ANOVA;  $F_{1,124} = 171$ ,  $P < 0.0001$ ), and distances to nearest intraspecific neighbour among *P. americana* were higher when *P. americana* encountered *P. australasiae* than when they encountered *B. orientalis* (ANOVA;  $F_{1,745} = 45$ ,  $P < 0.0001$ ) (Figure 4). These distances were also higher when *P. americana* were residents than when they were intruders (ANOVA;  $F_{1,745} = 22$ ,  $P < 0.0001$ ). During interspecific encounters, modifications of shelter access were observed in relation to pairs of species. *Periplaneta americana* had priority access to shelter over *B. orientalis* and *P. australasiae*. *Periplaneta americana* maintained their shelter occupancy by modifying their tolerable inter-individual distance in relation to their resident status and in relation to species encountered.

The presence of a second shelter increased the total numbers of sheltered individuals (ANOVA;  $F_{1,258} = 69.9$ ,  $P < 0.0001$ ) (Figure 2). As previously observed, distances to nearest intraspecific neighbour were shorter than distances to nearest interspecific neighbour (ANOVA;  $F_{1,3367} = 808$ ,  $P < 0.0001$ ). In *P. americana*–*B. orientalis* encounters, the proportions of sheltered individuals increased for both species, indicating that both benefited from the presence of the second shelter (t-test; *P. americana*:  $t = 4.89$ , d.f. = 86,  $P < 0.0001$ ; *B. orientalis*:  $t = -6.97$ , d.f. = 86,  $P < 0.0001$ ). In *P. americana*–*P. australasiae* encounters, the proportions of sheltered individuals only increased for *P. australasiae*



**Figure 4** Distances (means + SE) in cm to nearest neighbours during interspecific encounters. (A) *P. americana*–*B. orientalis* encounters: distance to nearest intraspecific neighbour (black bars) and distance to nearest interspecific neighbour (striped bars) for *B. orientalis* individuals (*B. orientalis*–*P. americana*) and for *P. americana* individuals (*P. americana*–*B. orientalis*). (B) *P. americana*–*P. australasiae* encounters: distance to nearest intraspecific neighbour (black bars) and distance to nearest interspecific neighbour (striped bars) for *P. americana* individuals (*P. americana*–*P. australasiae*) and for *P. australasiae* individuals (*P. australasiae*–*P. americana*).

(t-test;  $t = -6.94$ , d.f. = 57,  $P < 0.0001$ ), but remained stable for *P. americana* (t-test;  $t = -1.32$ , d.f. = 57,  $P = 0.193$ ). Therefore, we concluded that *P. americana* did not modify their resting behaviour during encounters with *P. australasiae*, because the presence of *P. australasiae* did not limit the access of *P. americana* to the shelters.

Fewer *B. orientalis* or *P. australasiae* individuals were observed in shelters preferentially occupied by *P. americana* than in the other shelters (ANOVA;  $F_{1,126} = 46.9$ ,  $P < 0.0001$ ). The presence of the second shelter decreased interspecific competition, enabled more individuals to gain access to a shelter, and induced spatial segregation between the two species. Under these conditions, *B. orientalis* and *P. australasiae* benefited from better shelter access than when shelter space was limited.

**Food access.** During *P. americana*–*B. orientalis* encounters the proportions of individuals of both species present on the food source were significantly less than in intraspecific

encounters (t-test; *P. americana*:  $t = -7.86$ , d.f. = 1418,  $P < 0.0001$ ; *B. orientalis*:  $t = -4.81$ , d.f. = 1378,  $P < 0.0001$ ) (Figure 3). The temporal distribution of food intake of either species was not modified during interspecific encounters compared to intraspecific encounters. Maximum food intake still occurred during the first observation hour for both species (ANOVA; *B. orientalis*:  $F_{1,2686} = 5.8$ ,  $P = 0.017$ ; *P. americana*:  $F_{1,2576} = 38.8$ ,  $P < 0.0001$ ). The co-occurrence of both species on the food source was very high and reached 90%. The addition of a second food source allowed more cockroaches to gain access to food than when only one source was present (ANOVA;  $F_{1,3356} = 757$ ,  $P < 0.0001$ ) (Figure 3). In this case, co-occurrences of both species decreased significantly (t-test;  $t = 3.34$ , d.f. = 2,  $P < 0.001$ ). Doubling the number of food sources facilitated access for more individuals of each species, inducing a decline of co-occurrence and enhancing segregation among species.

During *P. americana*–*P. australasiae* encounters, the proportions of *P. americana* on food sources increased compared to those observed in *P. americana* intraspecific encounters (t-test;  $t = 16.35$ , d.f. = 838,  $P < 0.0001$ ), whereas the proportions of *P. australasiae* declined (t-test;  $t = -12.7$ , d.f. = 638,  $P < 0.0001$ ) (Figure 3). The temporal distributions of food intake were modified during interspecific encounters: maximum food intake by *P. australasiae* shifted from the first to the second observation hour (ANOVA;  $F_{1,636} = 16.3$ ,  $P < 0.0001$ ), whereas, for *P. americana*, maximum food intake remained in the first observation hour (ANOVA;  $F_{1,836} = 412$ ,  $P < 0.0001$ ). The co-occurrence of both species on a food source was only 54%. As the numbers of *P. americana* on a food source increased, the numbers of *P. australasiae* declined (correlation coefficient =  $-0.90$ ,  $P < 0.05$ ). Both species modified their feeding behaviour. *Periplaneta americana* dominated food access by increasing time they spent feeding, thereby preventing *P. australasiae* from gaining access to the food source.

## Discussion

Our experiments investigated the outcome of intra- and interspecific encounters among several urban cockroach species during the exploitation of two limiting resources: shelter and food, under laboratory conditions.

During intraspecific encounters the limited size of the shelters constrained some individuals to stay outside. The observed interindividual distances agree with an interindividual tolerance level, above which some individuals preferred to stay outside rather than to tolerate shorter interindividual distances. Each species has its own tolerance level: *P. australasiae* had the lowest tolerance level with a high mean interindividual distance ( $2.20 \pm 0.08$  cm), *B. orientalis*

had the highest tolerance level with a short mean interindividual distance ( $1.16 \pm 0.06$  cm), and *P. americana* had an intermediate mean interindividual distance ( $1.41 \pm 0.03$  cm). Prior residency gave no advantage for shelter access. Residents and conspecific intruders mixed homogeneously inside the shelters. All three species behaved similarly. No asymmetry in contests among residents and intruders could be seen (Maynard-Smith & Parker, 1976). The presence of each individual in a shelter was essentially the result of interindividual interactions (Breed et al., 1975, 1981; Deleporte, 1982; Rivault & Cloarec, 1990).

During interspecific encounters, observed modifications in shelter occupancy revealed that individuals of each interacting species were well aware of the presence of non-conspecifics. Furthermore, individuals of the same species stayed closer to one another, and as a consequence, species segregation appeared inside the shelter. Two types of specific profiles could be defined. *Periplaneta americana* maintained their shelter occupancy unchanged, whereas shelter access was impaired for *B. orientalis* and *P. australasiae*. Whether they were residents or intruders, *P. americana* always modified their tactics by adjusting interindividual distances to maintain a constant presence in the shelters. Residents resisted non-conspecific newcomers by increasing their interindividual distances so as to occupy the largest possible area, while intruders lowered theirs to ensure shelter access to as many conspecifics as possible. Furthermore, the behaviour of *P. americana* differed in relation to the species encountered. *Periplaneta americana* resisted *P. australasiae* because they left the smallest possible space free in the shelter, and because the low tolerance level of *P. australasiae* prevented them from entering the shelter. When encountering *B. orientalis*, *P. americana* had to draw closer to one another to maintain their presence in the shelters. Thus it seemed that *P. americana* were more compressed by the presence of *B. orientalis*, which have a lower interindividual tolerance level. Similarly, observed modifications in food access revealed that individuals of each interacting species were aware of the presence of non-conspecifics. Nevertheless, high co-occurrence levels of *P. americana*–*B. orientalis* pairs during food exploitation indicated a high tolerance between the two species. The presence of *P. americana* on the food source in *P. americana*–*P. australasiae* encounters prevented *P. australasiae* from gaining access to food. This situation might be the result of interference competition, where individuals interact directly with one another and prevent opponents from exploiting resources (Begon et al., 1986). Interspecific competition induced *P. australasiae* to delay their maximum food intake in the presence of *P. americana*. This temporal segregation gave priority access to *P. americana* and this could become detrimental for *P. australasiae* if resources are limited.

Decrease of shelter or food access by one species of the tested pairs indicated that dominant/subordination relationships exist among species. The inability of the subordinate species to maintain their resource exploitation level suggested that they risked exclusion under more constraining conditions. Nevertheless, the presence of a second shelter or a second food source enhanced the spatial segregation between two competing species. As a consequence, more individuals gained access to the resource and the subordinate species was able to exploit areas not occupied by the dominant species. Therefore, increasing the number of available resources facilitated the coexistence of competing species (Atkinson & Shorrocks, 1981). Observed interference during food or shelter exploitation among sympatric urban cockroach species indicated strong asymmetries among species and a tendency to develop spatial or temporal segregation. The fact that spatial segregation occurred at different scales inside and between shelters under our experimental conditions, means that competition occurred among species. The consequences of species competition were amplified by dominant/subordination relationships among species. These behavioural mechanisms, which shaped species distributions under experimental conditions, might explain, at least partly, the observed distributions of urban cockroach species at the flat or building levels within a given town. *Blatta orientalis* are often displaced when forced to share harbourages with *P. americana* (Robinson, 1996). Although our experimental results indicate that *P. americana* largely dominate *P. australasiae*, the fact that *P. americana* and *P. australasiae* have been reported to be caught in the same baited traps in Australia could be explained by a transitory situation that could lead to the exclusion of one species by the other (Miller & Peters, 1999). One particular trait of microhabitats exploited by cockroaches in urban areas is their patchiness, as each building constitutes an isolated patch where active movements of cockroaches inside one building occur at low rates (Thoms & Robinson, 1987; Brenner, 1988; Rivault, 1990; Cloarec et al., 1999). Active movements have not been seen among buildings, particularly in temperate areas where transfers rely mainly on passive human transport (Rivault, 1991; Cornwell, 1968). The keys to the success of urban cockroach species are their capacities to tolerate changing environments and to utilize the food available in human living areas (Robinson, 1996). Although physiological and ecological data stress species differences (Appel, 1991), parameters defining their habitat selection largely overlap. In addition, these urban species tolerate a wide range of temperatures and humidity (Cornwell 1968). Furthermore, our experimental results stress the importance of interspecific competition in shaping the distributions of different species. When access to resources is limited, interspecific competition occurs

among species with overlapping distributions and similar ecological requirements, and one species has priority access to the most important resources; this can become detrimental for the subordinate species. Improvements in urban cockroach pest control and the development of integrated pest management would benefit from a better knowledge of the life history traits of the different species and their spatial dynamics (Brenner et al., 1998).

## References

- Albrecht M & Gotelli NJ (2000) Spatial and temporal niche partitioning in grassland ants. *Oecologia* 26: 134–141.
- Appel AG (1991) Water relations and thermal sensitivity of several cockroach species (Dictyoptera: Blattidae and Blaberidae). *Comparative Biochemistry and Physiology* 100A: 353–356.
- Atkinson WD & Shorrocks B (1981) Competition on a divided and ephemeral resource: a simulation model. *Journal of Animal Ecology* 50: 461–471.
- Ayala FJ (1969) Experimental invalidation of the principle of competitive exclusion. *Nature* 224: 1076–1079.
- Begon M, Harper JL & Townsend CR (1986) *Ecology: Individuals, Populations and Communities*. Blackwell Scientific Publications, Oxford, UK.
- Bell WJ & Adiyodi KG (1981) *The American cockroach*. Chapman and Hall, New York.
- Breed MD, Hinkle CM & Bell WJ (1975) Agonistic behavior in the German cockroach, *Blattella germanica*. *Zeitschrift für Tierpsychologie* 39: 24–32.
- Breed MD, Meaney C, Deuth D & Bell WJ (1981) Agonistic interactions of two cockroaches species, *Gromphadorina portentosa* and *Supella longipalpa* (Orthoptera, Dictyoptera: Blaberidae, Blattellidae). *Journal of the Kansas Entomological Society* 54: 197–208.
- Brenner RJ (1988) Focality and mobility of some peridomestic cockroaches in Florida (Dictyoptera: Blattaria). *Annals of the Entomological Society of America* 81: 581–592.
- Brenner RJ, Focks DA, Arbogast RT, Weaver DK & Shuman D (1998) Practical use of spatial analysis in precision targeting for integrated pest management. *American Naturalist* 44: 79–101.
- Capowiez Y (2000) Differences in burrowing behaviour and spatial interaction between the two earthworm species *Aporrectodea nocturna* and *Allobophora chlorotica*. *Biology and Fertility of Soils* 30: 341–346.
- Clark PJ & Evans FC (1954) Distance to nearest neighbour as a measure of spatial relationships in populations. *Ecology* 35: 445–453.
- Cloarec A, Rivault C & Cariou ML (1999) Genetic population structure of the German cockroach, *Blattella germanica*: Absence of geographical variation. *Entomologia Experimentalis et Applicata* 92: 311–319.
- Cornwell PB (1968) *The Cockroach*. Vol. 1: A Laboratory Insect and an Industrial Pest. Hutchinson & Co., London, UK.
- Deleporte P (1982) Relations sociales et utilisation du milieu par des larves mâles du premier stade chez *Periplaneta americana* (Dict.) *Insectes Sociaux* 29: 485–510.

- Hardin G (1960) The competitive exclusion principle. *Science* 131: 1292–1297.
- Human KG & Gordon DH (1996) Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia* (Berlin) 105: 405–412.
- Maynard-Smith J & Parker GA (1976) The logic of asymmetric contests. *Animal Behaviour* 24: 159–175.
- Miller PF & Peters BA (1999) Performance of Goliath cockroach gel against German cockroach (Blattodea: Blattellidae) in the field. Proceedings of the 3rd International Conference on Urban Pests, Prague (Czech Republic) (ed. by WH Robinson, F Rettich & GW Rambo), pp. 153–169. Grafické Závody Hronov, Czech Republic.
- Pimentel D, Feinberg EH, Wood PW & Hayes JT (1965) Selection, spatial distribution, and the coexistence of competing fly species. *American Naturalist* 99: 97–109.
- Rivault C (1985) Rythme circadien de comportements: synchronisation par l'environnement physique et social chez 2 espèces de blattes. Thesis. Rennes University, France.
- Rivault C (1989) Spatial distribution of the cockroach, *Blattella germanica*, in a swimming-bath facility. *Entomologia Experimentalis et Applicata* 53: 247–255.
- Rivault C (1990) Distribution dynamics of *Blattella germanica* in a closed urban environment. *Entomologia Experimentalis et Applicata* 57: 85–91.
- Rivault C (1991) Invasion des milieux urbains par les blattes: exemple de la ville de Rennes. Colloque National d'Ecologie Urbaine Lyon (ed. by Université Claude Bernard Lyon I), pp. 145–156. Université de Lyon I, Lyon, France.
- Rivault C & Cloarec A (1990) Exploitation des ressources alimentaires par *Blattella germanica* dans une piscine. *Actes des Colloques Insectes Sociaux* 6: 91–98.
- Robinson WH (1996) *Urban Entomology. Insect and Mite Pests in the Human Environment*. Chapman & Hall, London, UK.
- Robinson WH, Rettich F & Rambo GW (1999) Proceedings of the 3rd International Conference on Urban Pests, Prague (Czech Republic). Grafické Závody Hronov, Czech Republic.
- Rust MK, Owens JM & Reiersen DA (1995) *Understanding and Controlling the German Cockroach*. Oxford University Press, Cambridge, UK.
- Sokal RR & Rohlf FJ (1981) *Biometry*, 2nd edn. W.H. Freeman & Co., New York, USA.
- StatView (1998) *User's Guide, Version 5.0*. SAS Institute, Cary, NC.
- Thoms EM & Robinson WH (1987) Insecticide and structural modification strategies for management of Oriental cockroach (Orthoptera: Blattidae) populations. *Journal of Economic Entomology* 80: 131–135.
- Willey KB (1996) Proceedings of the 2nd International Conference on Insect Pests in the Urban Environment, Edinburgh (Scotland). BPC Wheatons Ltd, Exeter, UK.
- Willey KB & Robinson WH (1993) Proceedings of the 1st International Conference on Insect Pests in the Urban Environment, Cambridge. BPC Wheatons Ltd, Exeter, UK.