Behav Ecol Sociobiol (1995) 37 : 393–398

Jaimie T.A. Dick · Robert W. Elwood · W. Ian Montgomery

The behavioural basis of a species replacement: differential aggresssion and predation between the introduced *Gammarus pulex* and the native *G. duebeni celticus* (Amphipoda)

Received: 23 June 1994/Accepted after revision: 14 August 1995

Abstract Previous studies have shown that differential predation by males on moulted female congenerics may be largely responsible for the elimination and replacement of the native Irish freshwater amphipod *Gammarus duebeni celticus* by the introduced *G. pulex*. Predation of moulted females occurs both shortly after their release from precopulatory mate-guarding and whilst they are being guarded by their mates. In the present study, two hypotheses concerning the underlying cause(s) of the differential predation pattern are tested. Firstly, female *G. d. celticus* may be more vulnerable to predation than female *G. pulex* due to the former being released from precopula guarding with the new exoskeleton in a less hardened state. Secondly, *G. pulex* may be an inherently more aggressive species than *G. d. celticus* during predatory interactions over guarded females. The first experiment indicated that differential predation was not mediated by species differences in the state of the female exoskeleton at the time of release from precopula by guarding males. The second experiment, however, showed that male *G. pulex* were significantly more aggressive than male *G. d. celticus* in attacking both guarding male congenerics and guarded moulted female congenerics. In addition, in defence against predatory attacks, paired male and female *G. pulex* were significantly more aggressive than paired male and female *G. d. celticus*. These differences in aggressive behaviour led to a significantly higher frequency of predation on *G. d. celticus* females than on *G. pulex* females, and also explains this finding in previous studies. It is concluded that differential predation due to differences in aggressive behaviour may explain the pattern of replacement between these species.

J.T.A. Dick (✉) · R.W. Elwood · W.I. Montgomery
Division of Environmental and Evolutionary Biology,
School of Biology and Biochemistry,
The Queen's University of Belfast,
Medical Biology Centre, 97 Lisburn Road,
Belfast BT9 7BL, Northern Ireland

Keywords Aggression · Amphipods · Predation · Species replacements

Introduction

The success of an invading species depends on the ability of individuals of that species to withstand the many ecological pressures of the new environment. These pressures may include direct behavioural interactions with native species, such as competition and predation. Species with inherently high aggressive tendencies, therefore, are often successful invaders (Elton 1958; Baker and Stebbins 1965; Ehrlich 1986; Drake et al. 1989; di Castri et al. 1990). For example, the Argentine ant (*Iridomyrmex humilis*) has invaded many regions of North America, its highly aggressive behaviour towards native ant species resulting in their displacement (Smith 1936; Elton 1958; Ward 1987).

For several years, we have monitored the continuing replacement of the native Irish freshwater amphipod *Gammarus duebeni celticus* Stock & Pinkster by an introduced congeneric, *G. pulex* (L.) (Dick et al. 1990a, 1993, 1994; see also Strange and Glass 1979). Differential predation between these species may explain this replacement, since *G. pulex* are more successful in both predating *G. d. celticus* and in avoiding being predated by their congenerics (Dick et al. 1990b, 1993; Dick 1992). In particular, males of each species kill and eat solitary moulting female congenerics, usually in 100% of trials (e.g. Dick 1992). However, moulting females are normally held by males in precopula guarding and this significantly reduces the frequency of female predation by congenerics in both species (Dick et al. 1990b, 1993). Nevertheless, female *G. d. celticus* are significantly more often killed and eaten by male congenerics than are female *G. pulex* (Dick et al. 1990b, 1993).

We have observed predation of moulted females both shortly after their release from the precopulatory mate-guarding phase and whilst those females were being actively guarded by their conspecific mates (Dick 1992). It is not known, however, at what stage the differential predation pattern arises. In the present study, we test two hypotheses concerning the underlying causes(s) of the higher success of *G. pulex* over *G. d. celticus* in predating female congenerics. Firstly, we sought to determine whether differential release times of females of the two species from precopula, relative to the hardening of the exoskeleton, results in differential female vulnerability to predation. This in itself may partly or wholly explain observed differences in predation frequencies. Secondly, differential predation may be the result of differences in the aggressive tendencies of the two species, in terms of attacking and/or defensive behaviour, during predatory interactions over guarded females.

Methods

In January-March 1991, specimens of *G. pulex* were collected from the River Ravarnet, a major tributary of the River Lagan, at Lisburn, Co. Down. *G. d. celticus* were collected from a small tributary at the upper reaches of the River Lagan, at Dromore, Co. Down, an area at the time not invaded by *G. pulex*. Subsequently, however, *G. pulex* has invaded this stream and other upper reaches of the Lagan system (see Dick et al. 1994).

In the laboratory, animals were kept in large aerated aquaria supplied with substratum, fauna and flora from the streams. Temperature and daylength were appropriate for the time of year and animals were allowed to acclimatize for 1 week prior to experiments. Both species were collected from clean freshwater and were observed to survive, feed and reproduce in each others' source water. Nevertheless, experiments were conducted in a 1:1 mixture of water from the two streams. This was designed to balance any effects of differences in water quality that may have advantaged either species.

Experiment 1

Twice daily, we inspected 60 precopula pairs of each species that had been individually placed in 5-cm–diameter plastic cups. When each female had moulted and, after copulation, was released by the guarding male, she was immediately presented to a congeneric male and the outcome recorded. This was designed to test the hypothesis that differential release times relative to exoskeleton hardening may result in differential predation frequencies. Male cannibalism of moulted female precopula partners sometimes occurs in these species (Dick 1995). In this study, this reduced the sample sizes to 52 trials for *G. pulex* and 49 trials for *G. d. celticus*.

Experiment 2

Large numbers of precopula pairs of each species were separated by placing the animals on tissue paper until the male released the female. Females were then weighed to the nearest 1 mg and isolated in 5-cm-diameter plastic cups. Males were held in stock tanks. The females were inspected twice daily and newly moulted animals selected for the experiments. Such females were presented to male conspecifics (weighed to nearest 1 mg) and allowed to form precopula. Such pairings normally result in copulations within 20 min and females are released within 12 h (see Dick and Elwood 1989a, b). Once precopula had been established for 5 min, a congeneric male (weighed to nearest 1 mg) was introduced to the pair in a petri dish (9 cm diameter/2 cm depth water) and behaviour recorded. This was done with a time/event programme on an Apple computer, observations being made for 30 min for each replicate. Table 1 presents details of activities recorded. There were 31 replicates of male *G. d. celticus* with a precopula pair of *G. pulex* and 35 replicates of the reciprocal interaction. The predatory struggles over moulted females closely resemble intraspecific fights for possession of females (see Dick and Elwood 1990; Dick 1992). Once the 30-min observation period had elapsed, the trio of animals were left together for a further 12 h (i.e. the maximum post-copula guarding time) and the outcome recorded.

Table 1 Behaviour recorded during predatory interactions (30 min observations)

1) No. of times male swims towards and contacts congeneric pair with antennae
3) No. of attacks directed at congeneric female (grabbing at female with gnathopods)
4) Time spent attacking female
5) No. of tugs at female when female grabbed
6) No. of attacks directed at congeneric guarding male
7) Time spent attacking guarding male
8) No. of defensive kicks by guarding male
9) No. of defensive kicks by guarded female

Results

Experiment 1

There was no significant difference in the numbers of females of the two species predated on presentation to a congeneric male following their release by the guarding conspecific male (22 of 52 *G. pulex* females were predated vs. 20 of 49 *G. d. celticus* females; $P = 1.0$, Fisher exact probability test). Thus, the differential predation frequencies noted previously (Dick 1992; Dick et al. 1993) do not appear to be a function of female vulnerability due to differential release times by guarding males. Newly released females of the two species appear to be equally vulnerable to congeneric predation.

Experiment 2

Body size differences between the species

It is generally known that adult *G. d. celticus* are, on average, larger than adult *G. pulex* (e.g. Dick et al. 1990b). This was the case in this study, with *G. d. celticus* males being significantly larger than *G. pulex* males (means ± S.E.; 81.9 ± 3.6 mg vs. 69.6 ± 1.9 mg; $t = 2.9$, $df = 60$, $P < 0.005$) and *G. d. celticus* females being significantly larger than *G. pulex* females (51.1 ± 2.33 mg vs. 36.8 ± 1.54 mg; $t = 5.1$, $df = 60$, $P < 0.0001$).

Table 2 Aggressive behaviour of *Gammarus pulex* and *G. d. celticus* during predatory interactions over guarded, recently moulted females. Means are given with SE in parentheses

	G. pulex	*G.d. celticus*	*df*	*t*	*P*
(a) Behaviour of attacking males					
No. antennal contacts of pairs	29.8 (2.9)	35.9 (3.3)	59	1.4	NS
No. attacks at females	6.5 (0.9)	3.5 (0.7)	60	2.3	< 0.025
Time attacking females (s)	22.5 (6.3)	7.2 (1.7)	60	2.4	< 0.025
No. tugs at females	3.8 (0.8)	0.7 (0.3)	60	3.7	< 0.001
No. attacks at males	11.4 (2.0)	5.8 (1.2)	60	2.3	< 0.025
Time attacking males (s)	52.6 (17.9)	13.8 (4.1)	60	2.0	< 0.02
Attacks at female/contact	0.3 (0.1)	0.1 (0.02)	59	2.4	< 0.025
Tugs at female/attack	0.6 (0.2)	0.2 (0.07)	50	2.2	< 0.02
Attacks at male/contact	0.3 (0.04)	0.2 (0.04)	59	2.5	< 0.02
(b) Behaviour of guarding males					
No. defensive kicks	66.9 (8.2)	52.8 (8.8)	60	1.15	NS
No. kicks/contact	1.7 (0.1)	1.6 (0.2)	59	0.5	NS
No. kicks/attack at female	30.8 (5.8)	10.1 (1.3)	51	3.8	< 0.001
No. kicks/attack at male	8.9 (3.3)	6.9 (1.9)	55	3.2	< 0.0025
(c) Behaviour of guarded females					
No. defensive kicks	6.3 (1.7)	1.7 (0.6)	60	2.6	< 0.02
No. kicks/contact	0.2 (0.04)	0.06 (0.02)	59	2.4	< 0.025
No. kicks/attack	2.7 (1.1)	0.3 (0.08)	51	2.5	< 0.02

Description and outcomes of predatory struggles

Typically, the attacking male would contact the congeneric pair with his antennae and attempt to grab either the male or the female. On grabbing the male, the attacker would bite at the congeneric, resulting in defensive kicking from the guarding male. On grabbing the female, the attacker would attempt to wrest the female from the guarding male by tugging at the female (see plate in Dick 1992). This resulted in defensive kicks from both male and female congenerics. Contact by the attacking male would often result in the defending congeneric male angling his female away from the attacker, together with defensive kicks at the attacker. Defending male *G. pulex* were particularly adept at keeping male *G. d. celticus* away from females in this manner. In addition, attacking males of both species would immediately bite at females on successfully grabbing hold of them.

Only one male *G. d. celticus* was successful in predating the guarded female congeneric within the 30-min observation period, whereas five male *G. pulex* were successful ($P = 0.1$, Fisher exact probability test). In three of the predatory take-overs by male *G. pulex*, the female was wrenched from the guarding congeneric male during violent struggles. In the other two take-overs, and the male *G. d. celticus* take-over of a female *G. pulex*, it was the guarding males that were initially attacked. This involved biting of the antennae, legs and uropods, to the extent that the guarding males released their females, which were then devoured by the male congeneric! Predation attempts were observed to continue after the 30-min observations such that, 12 h later, a total of six female *G. pulex* had been predated compared to 27 female *G. d. celticus* ($P < 0.0001$, Fisher test).

Behaviour of attacking males

Table 2a presents comparisons of the behaviour of attacking males of the two species. There was no

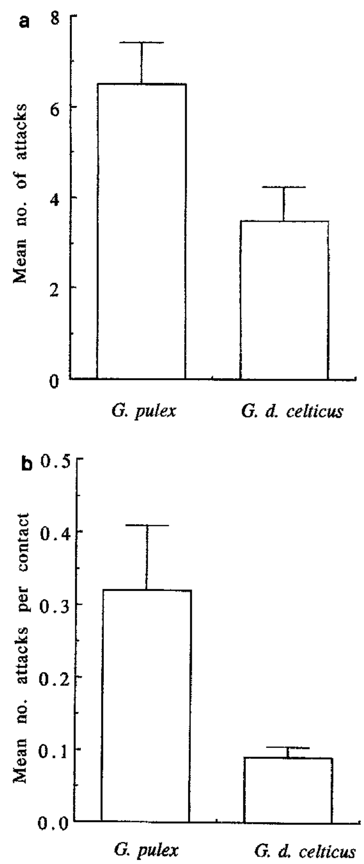

Fig. 1a Mean numbers (± SE) of predatory attacks directed at guarded moulted female congenerics by male *Gammarus pulex* and male *G. duebeni celticus* (see Table 2a). **b** Mean numbers (± SE) of predatory attacks per antennal contact (see Table 2a)

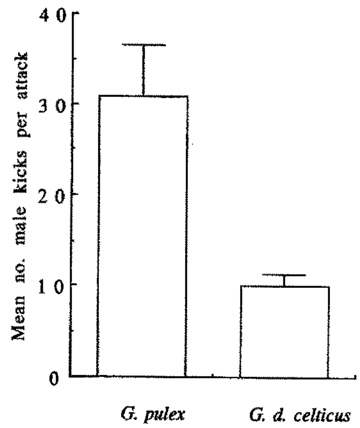

Fig. 2 Mean numbers (± SE) of defensive kicks by guarding males per attack on guarded females by congeneric males (see Table 2b)

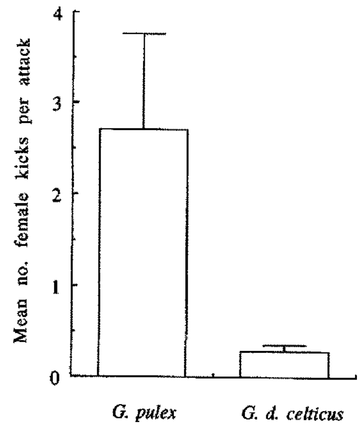

Fig. 3 Mean numbers (± SE) of defensive kicks by guarded females per attack by congeneric males (see Table 2c)

significant difference between males of the two species in the mean number of occasions, over 30 min, those males swam towards and contacted congeneric precopula pairs with the antennae. In addition, all but 1 of the 31 male *G. pulex* and all but 3 of the 35 male *G. d. celticus* attacked the congeneric pair at least once during the 30-min observation period. Thus, the general activity level of experimental animals did not differ between the species. Male *G. pulex*, however, directed attacks at female *G. d. celticus* significantly more often than male *G. d. celticus* directed attacks at female *G. pulex* (Fig. 1a). Male *G. pulex* consequently spent significantly more time directing attacks at congeneric females than did male *G. d. celticus*. Additionally, the higher level of attacking by male *G. pulex* resulted in these males tugging significantly more frequently at congeneric females in their attempts to steal the female. Male *G. pulex* also attacked guarding male congenerics significantly more often, and thus consequently for significantly longer, than did male *G. d. celticus*.

Male *G. pulex* thus made more attacks than male *G. d. celticus* during the 30-min observation periods. In addition, individual attacks by male *G. pulex* were more intense than were attacks by male *G. d. celticus* (Table 2a). Male *G. pulex*: (1) attacked female congenerics significantly more often per antennal contact (Fig. 1b); (2) tugged significantly more often per attack of females and (3) attacked male congenerics significantly more often per antennal contact.

Behaviour of guarding males

Table 2b presents comparisons of the behaviour of guarding males. Male *G. pulex* tended to kick at attackers more often during the 30-min observation periods than did guarding male *G. d. celticus*, however, this trend was not significant. There was no significant difference in the mean numbers of male defensive kicks per antennal contact of the guarding pair. However, in defence against attack, guarding male *G. pulex*: (1) kicked significantly more often per congeneric attack on the guarded female (Fig. 2) and (2) kicked significantly more often per attack directed at themselves. Thus, male *G. pulex* were more active in defence of females, and of themselves, than were male *G. d. celticus*.

Behaviour of guarded females

Table 2c presents comparisons of the behaviour of guarded females of the two species. Female *G. pulex* kicked at attacking congeneric males significantly more often during the 30-min observation periods than did female *G. d. celticus*. In addition, guarded female *G. pulex*: (1) kicked significantly more often per congeneric antennal contact of the pair and (2) kicked significantly more often per attack on themselves (Fig. 3). Thus, female *G. pulex* were more active in their own defence against predatory attack than were female *G. d. celticus*.

Discussion

The displacement, or replacement, of one animal species by another may be mediated by several mechanisms (e.g. Pontin 1982). Classically, resource exploitation and/or interference competition, predation and hybridization, often concomittant with habitat disturbances, are cited as probable mechanisms (e.g. Elton 1958; McDowall 1968; Moyle 1976; Taylor 1979; Nilssen et al. 1984; Diamond and Case 1986; Kitching 1986). Field surveys are able to identify patterns in species replacements and "natural" field-based experiments may detect niche shifts that are presumed to be due to interspecific competition. However, alternative processes such as predation may be responsible for such niche shifts and changes in patterns of distribution and abundance (Connell 1975; Heck 1980; Underwood

1986). Thus, the elucidation of mechanisms of elimination and replacement may often only be fully achieved by the complementary use of controlled laboratory experimentation and direct behavioural observations.

Our repeated field surveys have shown that *G. pulex* actively replaces *G. d. celticus* (Dick et al. 1993, 1994). We have also shown in laboratory experiments that differential predation between *G. pulex* and *G. d. celticus* is a likely causal factor in this replacement phenomenon (Dick et al. 1993). In particular, the rapid elimination of reproductive females is likely to have drastic population effects over time (see Dick et al. 1993). The present study has identified behavioural mechanisms that explain this greater ability of *G. pulex* over *G. d. celticus* with regard to predation of recently moulted female congenerics. Firstly, differential predation frequencies are not simply the result of female *G. d. celticus* being more susceptible to predation through being released from precopula at a more vulnerable stage of exoskeleton hardening (experiment 1). Rather, male *G. pulex* are more aggressive towards both male and female *G. d. celticus* engaged in precopula guarding than are male *G. d. celticus* in the reciprocal interaction (experiment 2). This results in greater numbers of female *G. d. celticus* than female *G. pulex* being killed and eaten. This situation is exacerbated by both male and female *G. pulex* in precopula pairs being more active in defence against predatory attack by congeneric males than are paired male and female *G. d. celticus*. It thus appears that *G. pulex* is an inherently more aggressive species than is *G. d. celticus*, resulting in differential predation on moulting females. This ability of *G. pulex* to overcome *G. d. celticus* in individual aggressive/predatory encounters is all the more remarkable considering that the latter species is substantially larger than the former.

In the time between conducting the above experiments and submitting this paper, *G. pulex* has invaded previously pure populations of *G. d. celticus*, including the collection site mentioned above, in some cases totally eliminating and replacing the native (see Dick et al. 1994). Such rapid eliminations are often associated with highly aggressive species with the ability to actively drive out native species, through competition for resources and/or direct predatory interactions (e.g. Smith 1936; Elton 1958; Bovbjerg 1970; Zaret and Paine 1973; Capelli and Munjal 1982; Pontin 1982; Moyle 1986; Kitching 1986; Ward 1987; Carlton 1989; Drake et al. 1989; di Castri et al. 1990). We do not deny that there may be resource competition between these two *Gammarus* species. However, we have mathematically modelled the community-level effects of resource competition operating alongside mutual predation (Dick et al. 1993). Simulations of this model revealed that differential mutual predation overrides the effects of resource competition, with the superior predator eliminating the inferior predator regardless of relative competitive abilities (Dick et al. 1993). Polis et al. (1989) reached similar conclusions based on several different mathematical approaches.

We thus conclude that males of the introduced *G. pulex*, being an inherently more aggressive species, kill and eat more females of the native *G. d. celticus* than *vice versa*. This differential predation of reproductive females is likely to lead to the rapid elimination of *G. d. celticus* populations and their subsequent replacement with *G. pulex* populations. We believe that studies of the behaviour of individuals, integrated with studies at the population and community levels, have successfully bridged the gap between pattern and process in this replacement pheneomenon. Such integrated approaches may be useful in understanding the numerous other cases of replacement observed over a range of animal taxa.

Acknowledgements We thank the Natural Environment Research Council for funding this work. John O'Kane, Dirk Platvoet and Sjouk Pinkster were helpful in a variety of ways in the production of the manuscript.

References

Baker HG, Stebbins GL (eds) (1965) The genetics of colonizing species. Academic Press, New York

Bovbjerg RV (1970) Ecological isolation and competitive exclusion in two crayfish (*Orconectes virilis* and *Orconectes immunis*). Ecology 51:225–236

Capelli GM, Munjal BL (1982) Aggressive interactions and resource competition in relation to species displacement among crayfish of the genus *Orconectes*. J Crust Biol 2:486–492

Carlton JT (1989) Man's role in changing the face of the ocean: biological invasions and implications for conservation of near shore environments. Conserv Biol 3:265–273

Castri F di, Hansen AJ, Debussche M (eds) (1990) Biological invasions in Europe and the Mediterranean basin (Monographiae Biologicae 65). Kluwer, The Netherlands

Connell JH (1975) Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: Cody M, Diamond J (eds) Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, pp 460–490

Diamond JM and Case TJ (1986) Overview: introductions, extinctions, exterminations and invasions. In: Diamond JM, Case TJ (eds) Community ecology. Harper and Row, New York, pp 65–79

Dick JTA (1992) The nature and implications of differential predation between *Gammarus pulex* and *G. duebeni celticus* (Crustacea: Amphipoda). J Zool Lond 227:171–183

Dick JTA (1995) The cannibalistic behaviour of two *Gammarus* species (Crustacea: Amphipoda). J Zool Lond 236:697–706

Dick JTA, Elwood RW (1989a) Assessments and decisions during mate choice in *Gammarus pulex* (Amphipoda). Behaviour 109:235–246

Dick JTA, Elwood RW (1989b) The causal and functional organization of mating behaviour in *Gammarus pulex* (Amphipoda). Behav Process 20:111–123

Dick JTA, Elwood RW (1990) Symmetrical assessment of female quality by male *Gammarus pulex* (Amphipoda) during struggles over precopula females. Anim Behav 40:877–883

Dick JTA, Elwood RW, Irvine DE (1990a) Displacement of the native Irish freshwater amphipod *Gammarus duebeni* by the introduced *G. pulex*. Ir Nat J 23:313–316

Dick JTA, Irvine DE, Elwood RW (1990b) Differential predation by males on moulted females may explain the competitive displacement of *Gammarus duebeni* by *G. pulex* (Crustacea: Amphipoda). Behav Ecol Sociobiol 26:41–45

Dick JTA, Montgomery I, Elwood RW (1993) Replacement of the indigenous amphipod *Gammarus duebeni celticus* by the introduced *G. pulex*: differential cannibalism and mutual predation. J Anim Ecol 62:79–88

Dick JTA, Elwood RW, Montgomery WI (1994) Range expansion of the alien amphipod *Gammarus pulex* in the River Lagan, Co. Down. Ir Nat J 24:403–404

Drake JA, Mooney HA, Castri F di, Groves RH, Kruger FJ, Rejmanek M, Williamson M (eds) (1989) Biological invasions – a global perspective (Scientific committee on problems of the environment SCOPE 37). John Wiley, Chichester

Ehrlich PR (1986) Which animal will invade? In: Mooney HA, Drake JA (eds) Ecology of biological invasions of North America and Hawaii (Ecological studies 58). Springer, Berlin Heidelberg New York, pp 79-95

Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London

Heck KL (1980) Competitive exclusion or competitive delusion? Paleobiology 6:241–242

Kitching RL (1986) Prey-predator interactions. In: Kikkawa J, Anderson DJ (eds) Community ecology. Pattern and process. Blackwell, Oxford, pp 214–239

McDowall RM (1968) Interactions of the native and alien faunas of New Zealand and the problems of fish introductions. Trans Am Fish Soc 97:1–11

Moyle PB (1976) Fish introductions in California: History and impact on native fishes. Biol Conserv 9:101–118

Moyle PB (1986) Fish introductions into North America: patterns and ecological impact. In: Mooney HA, Drake JA (eds) Ecology of biological invasions of North America and Hawaii (Ecological studies 58). Springer, Berlin Heidelberg New York, pp 27–43

Nilssen JP, Østdahl T, Potts WTW (1984) Species replacements in acidified lakes: physiology, predation or competition? Rep Inst Freshwater Res Drottningholm 61:148–153

Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. Annu Rev Ecol Syst 20:297–330

Pontin AJ (1982) Competition and coexistence of species. Pitman, London

Smith MR (1936) Distribution of the Argentine ant in the United States and suggestions for its control and eradication. Circ US Dept Agric 387:1–39

Strange CD, Glass GB (1979) The distribution of freshwater gammarids in Northern Ireland. Proc R Ir Acad 79B:145–153

Taylor JC (1979) The introduction of exotic plant and animal species into Britain. Biologist 26:229–236

Underwood T (1986) The analysis of competition by field experiments. In: Kikkawa J, Anderson DJ (eds) Community ecology. Pattern and process. Blackwell, Oxford, pp 240–268

Ward PS (1987) Distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the lower Sacramento Valley and its effects on the indigenous ant fauna. Hilgardia 55:1–17

Zaret TM, Paine RT (1973) Species introductions in a tropical lake. Science 182:449–455

Communicated by G.M. Klump