Animal Behaviour 79 (2010) 281–289

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Contest behaviour of maize weevil larvae when competing within seeds

Nelsa Maria P. Guedes[a,b], Raul Narciso C. Guedes[a,b,*], James F. Campbell[b,1], James E. Throne[b,1]

[a] Departamento de Biologia Animal, Universidade Federal de Viçosa
[b] USDA-ARS Grain Marketing and Production Research Center, Manhattan, Kansas

ARTICLE INFO

Article history:
Received 23 June 2009
Initial acceptance 22 July 2009
Final acceptance 1 October 2009
Available online 14 December 2009
MS. number: A09-00418R1

Keywords:
competition strategy
Curculionidae
interaction
intraspecific competition
life-history trait
maize weevil
resource monopolization
scramble competition
Sitophilus zeamais
Zea mays

Food limitation induces severe competition for obligate seed-feeding insect larvae that are unable to leave the seed selected by their mother. The number of eggs laid per seed and the number of larvae hatched from the eggs are important determinants of whether larval behaviour within the seed will be of the scramble or the contest type. In maize weevils, *Sitophilus zeamais*, few adults emerge per seed regardless of the number of eggs laid, which may arise from scramble competition, if the optimum egg density (i.e. egg density leading to maximum total larval fitness) is low compared to the number of eggs laid per seed, or from contest competition due to direct interference among the larvae. The behavioural process and the ecological outcome of competition were assessed in two strains of the maize weevil. Neither strain showed a reduction in body mass with increased competition, and they had similar optimal egg densities (two eggs per seed). There was a hump in the larval fitness curve suggesting a scramble competition, but this conclusion is compromised because the optimum egg density was small (two eggs per seed). X-ray imaging of seeds was used to observe interactions of larvae within the seed and showed direct interference, with aggression among the larvae. This provides evidence of contest-like competition within seeds even when egg density was low. Hence, one should be cautious in inferring the underlying type of competitive behaviour from variables such as body mass and initial egg density per seed. Direct observation of behaviour is required to make such an inference.

Local resource competition may lead to the selection of specific adaptive behaviour to overcome harmful interference among individuals (Sanz & Gurrea 2000; Alves-Costa & Knogge 2005), and this may have consequences for life-history traits (Smith & Lessells 1985; Smith 1990, 1991). Nicholson (1954) originally defined two distinct strategies of intraspecific competition, scramble and contest, which are frequently recognized in terms of resource use (e.g. Varley et al. 1973; Lomnicki 1988). In scramble competition, all members of a population have equal access to a limited resource, whereas under contest competition some members of a population (the winners) secure the available resource for their survival and reproduction, unlike others (the losers), who die.

The resource-limitation concept of competition is population-based. However, Nicholson (1954) also recognized the process by which competition takes place (i.e. its behavioural mechanism). The process of scramble competition takes place when there is accommodation of all competitors within a resource patch. The scramble process allows increased survival, but with reduced individual resource gain and consequently lower body mass gain with development, unlike in contest competition (Bakker 1961; Miller 1967; De Jong 1976; Giga & Smith 1991; Toquenaga 1993; Jansen & Sevenster 1997; Lale & Vidal 2001; Guedes et al. 2007). Contest competition implies direct interference among competitors (i.e. behavioural interference, such as aggressive attack) and typically only a single winner per territory (De Jong 1976; Smith & Lessells 1985; Guedes et al. 2007; Mano et al. 2007). The proximate behaviour underlying competition is, however, poorly studied, particularly for seed beetles (Guedes et al. 2003, 2007; Alves-Costa & Knogge 2005). This is because competition strategies are usually inferred from their final outcome: the relationship of the number (or fitness) of surviving individuals to the initial number entering the limited resource (Varley et al. 1973; Bellows 1982; Guedes et al. 2003).

There have been proximal studies of larval competition with the cowpea weevil, *Callosobruchus maculatus* (F.) (Coleoptera: Bruchidae), in which contest competition prevails in small host seeds (Messina 1991, 2004). Preliminary investigation of a 'contest' strain of *C. maculatus* indicated that vibrations are likely to mediate the process of competition, leading the dominant larva delaying the development of the conspecifics (Thanthianga & Mitchell 1987), although no playback studies were carried out to confirm this

* Correspondence: R. N. C. Guedes, Departamento de Biologia Animal, Universidade Federal de Viçosa, Viçosa, MG 36571-000, Brazil.
E-mail address: guedes@ufv.br (R.N.C. Guedes).
[1] J. F. Campbell and J. E. Throne are at the USDA-ARS Grain Marketing and Production Research Center, Manhattan, KS 66502, U.S.A.

0003-3472/$38.00 © 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2009.10.022

hypothesis. High feeding and respiration rates were also associated with contest competition in another strain of *C. maculatus* collected in lentils (Credland & Dick 1987; Daniel & Smith 1994; Guedes et al. 2003). In contrast, recent recognition of wall-making behaviour associated with 'scramble' strains of *C. maculatus* indicates that such behaviour may minimize direct interference among larvae, favouring similar resource partitioning among them and consequently leading to a scramble outcome of competition (Mano & Toquenaga 2008a, b).

The distinction between the behavioural process of competition and the ecological outcome after competition is essential (Smith & Lessells 1985; Smith 1990; Guedes et al. 2007). Although the process of competition results from intrinsically disruptive selection, the outcome also depends on the amount of resource required for development relative to its availability (Smith & Lessells 1985). A contest outcome may result even from a scramble process (i.e. without behavioural interference) depending on the resource availability and proximal mechanism involved, with consequences on life-history evolution (Smith 1990; Colegrave 1994, 1997; Nylin 2001; Guedes et al. 2003, 2007). For example, the large larvae with high metabolic rate from some strains of *C. maculatus* present a contest-like outcome of competition despite showing a scramble process of competition (Credland et al. 1986; Daniel & Smith 1994; Guedes et al. 2003).

Intensive selection is to be expected when resource units are discrete. This is the case for seeds parasitized by seed beetles that spend their larval stages within a single seed selected by their mother. Thus, the seed is a closed system within which the young larvae are unable to avoid competition with each other when multiple eggs are laid per seed (Smith 1990, 1991; Colegrave 1994). Seed beetles, such as the maize weevil, *Sitophilus zeamais* Motschulsky (Coleoptera: Curculionidae), can lay multiple eggs in a seed, thus increasing competition among the larvae within the seed (Smith & Lessells 1985; Danho et al. 2002; Danho & Haubruge 2003a). Females of this species tend to cluster their eggs in a few seeds subjected to multiple visits, which may also be the target of further egg-laying by other females (Smith & Lessells 1985; Danho & Haubruge 2003a, b), as was also reported for the related species *Sitophilus granarius*, the granary weevil (Fava & Burlando 1995). Clustered egg distributions of the maize weevil may be less common in the natural environment because fewer than two eggs per seed is usually observed, in contrast with laboratory studies (Throne 1994; Danho et al. 2002; Danho & Haubruge 2003a).

The maize weevil is an insect pest of cereals throughout agricultural regions of the world. There are large strain differences, most likely resulting from the way they are managed as pests (e.g. insecticide resistance; Fragoso et al. 2003, 2005; Guedes et al. 2006; Araújo et al. 2008; Guedes et al. 2009a). These strain differences may also arise because of the discontinuous nature of the stored seed environment. This probably accentuates seasonal population cycles. Such cycles lead to bottlenecks in population size, so that only small numbers of individuals establish new populations (Tanaka 1990; Tran & Credland 1995; Guedes et al. 1997). Few individuals emerge from seeds infested by more than one larva of this species (Throne 1994; Danho et al. 2002; Danho & Haubruge 2003a). The low rate of adult emergence in the maize weevil may result either from a scramble process, with a low (optimum) egg density leading to a peak in larval fitness, or from a contest process of competition with direct interference among the larvae. Both processes may generate a scramble outcome with an optimum egg density (i.e. egg density leading to maximum total larval fitness), but scramble competition reduces individual resources, again leading to lower adult body mass at emergence, unlike contest competition (Bakker 1961; De Jong 1976; Giga & Smith 1991; Jansen & Sevenster 1997; Guedes et al. 2007). The behavioural process and the ecological outcome of competition were assessed in two strains of the maize weevil. One of the strains is resistant to insecticides, but with no fitness disadvantage associated with this trait, probably because of its higher food consumption and higher energy metabolism (Guedes et al. 2006; Araújo et al. 2008; Guedes et al. 2009b), which may impact its competitive ability as reported in *C. maculatus* (Credland & Dick 1987; Daniel & Smith 1994; Guedes et al. 2003).

The main objective of this study was to determine the ecological outcome and underlying behavioural process of larval competition in strains of a seed beetle, which are seldom considered simultaneously. Sequential X-ray images were used to characterize the larval interactions taking place within the seed and how they relate to quantitative determinations obtained in this investigation and commonly used (indirectly) to recognize the behavioural process of competition involved (Table 1). Existence of competition is recognized by the decrease in percentage of adults emerging as egg density in the parasitized seed increases, which was expected in the maize weevil regardless of the outcome and behavioural process involved. The competition outcome is recognized by the shape of the larval fitness curve (i.e. insect biomass produced per seed) as a function of egg density: a peak indicates scramble competition, whereas a plateau reached at high egg densities indicates contest competition. The contest outcome of competition can be achieved either through a contest type of behavioural process with direct interference between larvae or through high larval feeding and metabolic rates leading to quick resource depletion and high larval mortality (low adult emergence). The scramble outcome may also be achieved through either a scramble process (e.g. accommodation via wall-making behaviour isolating the individual larva) or a contest-behavioural process.

The contest-behavioural process of competition implies direct interference among larvae favouring the dominant larva, but impairing the development of the others, which is more likely to take place when the insects show higher food consumption and, therefore, higher metabolism (determined as respiration rate) and weight gain. Such direct interference or encounter among larvae may result in active aggression and even cannibalism, but evidence for these in seed beetles is lacking. The low rate of adult emergence

Table 1
Quantitative predictions as a function of egg density used (indirectly) to recognize the behavioural process and ecological outcome of competition

Trait	Competition outcome			
	Scramble		Contest	
	Scramble process	Contest process	Scramble process	Contest process
Relative adult emergence per seed (%)	Decrease	Decrease	Decrease	Decrease
Absolute adult emergence per seed	Decrease	Decrease	Decrease	Does not vary
Larval competition curves	Peak	Peak (at low densities)	Plateau (at high densities)	Plateau (at high density)
Body mass	Decrease	Does not vary	Decrease	Does not vary
Respiration rate	Lower regardless of egg density	Higher regardless of egg density	Higher regardless of egg density	Higher regardless of egg density