

Population ecology of *Heteronyx piceus* (Coleoptera: Scarabaeidae) in a peanut/maize cropping system

A.L. Ward^{1†} and D.J. Rogers^{2‡*}

¹Farming Systems Institute, Queensland Department of Primary Industries, PO Box 23, Kingaroy, Queensland 4610, Australia: ²Farming Systems Institute, Department of Primary Industries, 80 Meiers Rd, Indooroopilly, Queensland 4067, Australia

Abstract

Large larval populations of the scarabaeid beetle *Heteronyx piceus* Blanchard that occur under peanuts, but not maize, in the South Burnett region of Australia are the result of a high rate and prolonged period of egg production by females feeding on peanut foliage. *Heteronyx piceus* is a relatively sedentary species and movement of females between adjacent fields is low. Populations of *H. piceus* varied markedly with landscape position. High larval populations are more likely (1 in 4 chance) to be encountered on the 'scrub' soils in the upper parts of the landscape than in the 'forest' soils in the lower half (1 in 20 chance), indicating that soil type/landscape position is a key risk factor in assessing the need for management intervention. The studies indicate that, because of the species' sedentary nature, the most meaningful population entity for management of *H. piceus* is the individual field, rather than the whole-farm or the region. The implications of this population ecology for management of the pest are discussed in relation to control strategies.

Keywords: *Heteronyx piceus*, peanut, soil type, landscape position, Australia, pest management

Introduction

Larvae of scarabaeid beetles (white grubs) have been recorded damaging peanuts in India (Yadava & Sharma, 1995), Israel (Harari *et al.*, 1997), and across East Asia and Africa (Wightman & Ranga Rao, 1994), as well as in both of the main peanut producing regions of Australia (Gough & Brown, 1988; Rogers *et al.*, 1992). The pest species attacking peanuts are often univoltine, and cause either direct root

damage (and thus plant death) (Yadava & Sharma, 1995), or attack the developing pods (reducing pod yield, but not plant density) (Rogers & Brier, 1992), or both. The severity and frequency of these reports indicate that peanuts are highly susceptible to white grub feeding, with even relatively low grub densities being capable of causing severe crop losses (Wightman & Ranga Rao, 1994; Yadava & Sharma, 1995; Rogers *et al.*, in press). Studies on population ecology of the white grubs in such systems provide important insights into factors that drive the development of damaging pest populations, and so lead to the development of rational and more sustainable management practices for these pests (Yadava & Sharma, 1995; Harari *et al.*, 1997; Litsinger *et al.*, 2002).

Heteronyx piceus Blanchard (Coleoptera: Scarabaeidae) is a medium-sized, summer-active, univoltine scarab that occurs in eastern Australia between the South Burnett region of Queensland and South Australia (Rogers *et al.*, 1992; Britton, 2000). Adults emerge in response to early summer storms

*Address for correspondence and

†Present address: BeckerUnderwood Australia, RMB 1084, Pacific Highway, Somersby, New South Wales 2250, Australia

Fax: +61 2 4340 2243

E-mail: andrew.ward@beckerunderwood.com

‡Present address: Research Connections and Consulting, PO Box 350, Toowong, Queensland 4066, Australia

(mid-October to late December) and feed (commonly on peanut foliage) before laying eggs under the crop row. Later instar larvae feed on developing peanut pods, prior to overwintering deep in the soil. Pupation occurs in early spring and adults remain in their pupal chambers until rain occurs (Rogers & Brier, 1992). This scarab is found commonly damaging peanuts in the South Burnett region of Queensland (Rogers *et al.*, 1992). Populations in excess of 4 larvae m^{-2} are common in the South Burnett and may reach over 30 larvae m^{-2} under some circumstances. Peanut yield reductions of up to 50% have been observed (Rogers & Brier, 1992). Prior to its emergence as a peanut pest in the South Burnett region, *H. piceus* was recorded once as an agricultural pest, attacking lucerne in Victoria (French, 1915).

The studies of *H. piceus* population ecology reported here are from an established peanut–maize cropping system in the South Burnett district of Queensland, Australia. They make clear why high *H. piceus* larval populations occur under peanut crops on some soils used for peanut production but not others, and also indicate why low populations occur under maize when adjacent peanut crops are heavily infested. The insights derived from these studies provide the basis for designing appropriate management tactics and strategies for this pest on peanuts.

Materials and methods

This study comprised four inter-linked experiments, three field, and one laboratory-based, conducted between late 1998 and mid-2001. The four experiments were:

1. District-wide surveys of *H. piceus* populations, to relate population size to landscape position/soil type.
2. Three seasons of systematic population sampling in five fields at one heavily infested site with a long history of crop damage.
3. Population movement studies to ascertain if populations under peanuts are maintained by adult *H. piceus* moving across crop interfaces, i.e. from where peanuts were grown last season to this year's peanuts.
4. Laboratory studies of fecundity and survival of adult *H. piceus* on a range of plant foods, to determine whether adult food is important to *H. piceus* reproductive success.

District survey

Third-instar *H. piceus* larval populations in the South Burnett region were sampled from peanut crops at 28 locations between 29 March and 1 April 1999, and again 8–17 March 2000. The sampling unit was a 30 cm square of soil centred on a randomly selected plant in the crop row, dug to plough depth and hand-sorted. Twenty samples were taken in each field. Larvae were fixed in KAA, and then transferred to 80% alcohol. In this survey, and the detailed studies at the Tingoora site, larvae of *H. piceus* were separated from other white grub species using the characters given in Rogers *et al.* (1992).

In the South Burnett region, peanuts are grown almost exclusively on soils derived from deeply weathered basalt (Sorby & Reid, 2001), and almost always in rotation with maize (Crosthwaite, 1994). For this reason, it was not possible to sample exactly the same area at each site in 1999 and 2000 (except for two sites that were double-cropped with peanuts). Rather, the closest possible peanut crop on

the same farm was sampled in 2000; this was almost always within 200 m of the 1999 sample. For analysis, samples were grouped by landscape position, as indicated by each site's Mapping Unit (Sorby & Reid, 2001): (i) pediments and mid-lower slopes; (ii) mid-upper slopes; and (iii) plateaux, hillcrests and upper hill slopes. The soils in pediments and mid-lower slopes are known locally as 'forest' soils, while the mid-upper slopes, plateaux and hillcrest soils are termed 'scrub' soils, reflecting the predominant original vegetation types (Vandersee & Kent, 1983).

Because a Spearman rank correlation for association between larval densities in the two years was non-significant ($P > 0.05$), the two-year's survey data were combined for the analysis of the effect of landscape position. The maximum-likelihood chi-square test was used to analyse the effect of landscape position on the frequency of sites over and under 4 larvae per row-metre, a larval population level associated with significant yield loss (based on the damage potential of *H. piceus* (Rogers *et al.*, in press)).

Tingoora study site

Detailed field studies were conducted on a commercial peanut farm at Tingoora, Queensland (latitude 26°20'51" S, longitude, 151°47'45" E). This farm was where *H. piceus* was first recorded as a peanut pest in 1962, and was a site that was included in the district survey. The study location was in an upper landscape position with a 'scrub' soil and was typical of the soils where *H. piceus* normally occurs in the South Burnett region (Rogers *et al.*, 1992). Insect count data from the Tingoora site were analysed by ANOVA and the protected LSD test after being transformed with the $\sqrt{(x+1/2)}$ transformation, except for adult flight trapping data which was transformed using the $\log_{10}(x+1)$ transformation.

Population dynamics

Populations of eggs, larvae and adults of scarab species were monitored in five adjacent fields at the Tingoora site from November 1998 to July 2001 to quantify population densities under the various crops over the three cropping seasons. It was not possible to speciate the scarab eggs, but larvae and adults were identified to species. Because white grub eggs were difficult to locate in the soil without resorting to complex and time-consuming sample processing procedures such as the turbulent overflow methods of Gough & Brown (1991), egg sampling efficiency was low.

The five fields included (i) four fields in a peanut/maize rotation, with two fields in peanuts each year, and (ii) one field (field 4) that had previously been in a long-term peanut/maize rotation, but which was sown to Rhodes grass (*Chloris gayana* Kunth (Poaceae)) after the 1995/96 cropping season. During the period of the study, it was in its third pasture year in the first sampling season, and then returned to the annual crop cycle. The details of the crop sequences in each field are given in table 1. A wheat crop followed each peanut crop during the study and was harvested before the summer maize crop. During winter, the white grub larvae were in hibernaculae below cultivation depth and are assumed not to have been directly affected by the wheat cultivation. After maize, fields were fallow over the winter and up to the planting of the next peanut crop.

Table 1. Crop sequences at Tingoorra, Queensland, Australia between 1998 and 2001.

Season	Field 1	Field 2	Field 3	Field 4	Field 5
1998/1999	Wheat–maize– winter fallow	Wheat–maize– winter fallow	Winter fallow– peanuts–wheat	Pasture (third year)	Winter fallow– peanuts–wheat
1999/2000	Peanuts–wheat	Peanuts–wheat	Maize–winter fallow	Peanuts–wheat	Maize–winter fallow
2000/2001	Maize–winter fallow	Maize–winter fallow	Peanuts–wheat	Maize–winter fallow	Peanuts–wheat

Each year, from the period from beetle emergence through to the start of the third instar, samples were taken from each field at approximately fortnightly intervals. When most larvae had reached third instar, the sampling frequency was reduced to monthly until the end of the cropping season. Over the winter, individuals are quiescent in cells in the soil, with most below normal sampling depth. During this period, sampling was less frequent. On each sampling date, samples were taken using the same procedures used in the district survey.

Heteronyx piceus movement across crop interfaces

Because the first year of population dynamics sampling documented high larval populations under peanuts, but not maize (fig. 2a), adult movement between fields 2 and 3 were studied in detail during the 1999/2000 and 2000/2001 seasons, as were end-of-season larval populations. These two fields are adjoining, each approximately 450 m wide and with a crop interface of approximately 1000 m.

Adult sampling was undertaken using a series of perspex window traps based on the design of Wilkening *et al.* (1981) (but without the upper collecting unit because *H. piceus* adults drop when they fly into an object rather than fly upwards). Each trap was 60 cm tall, 21 cm diameter, and attached to a plastic funnel over a bucket buried in the ground. The catching bucket contained a water/detergent mix to collect and kill beetles. Limited trapping up to a height of 2 m was conducted in 1999/2000 but very few females were trapped above 1.2 m. As a result, the adult-trapping study focused on traps situated on the ground.

Traps were arranged in three transects at 90° to the interface between fields 2 and 3. During the 1999/2000 summer, traps in both crops were located away from the crop interface every 20 m to 60 m, then every 40 m to 140 m. During the 2000/2001 season, the traps were located away from the crop interface into both crops every 20 m to 100 m, then every 40 m to 260 m. The traps were emptied at least twice a week, and daily after rainfall events. Trapped beetles were preserved in alcohol and subsequently sexed. Trapping concluded when the traps were obscured by the growing maize crop at about the end of January.

At the end of the 1999/2000 and 2000/2001 seasons, larval densities were sampled across the three adult-movement transects. Samples were taken at intervals on the transects, each sample being a 30 cm cube of soil centred on the crop row. In 1999/2000, samples were taken on either side of the crop interface at 10 m and 20 m, then every 20 m to 100 m, and then every 40 m to 300 m. In 2000/01, samples were taken on either side of the crop interface every 20 m out to 440 m from the interface.

Adult food and fecundity

This laboratory study examined the effect of peanut, maize, sorghum and soybean leaves (and a no-food control) on the fecundity and survival of *H. piceus* adults. Freshly emerged male and female beetles were placed in covered 150 mm diameter pots (two pairs per pot, 10 pots per treatment) that were half-filled with krasnozem soil maintained at 24% moisture (–200 kPa), a preferred moisture for oviposition in this soil (A.L. Ward and D.J. Rogers, unpublished data), and 25°C. Each female beetle was weighed at the start of the experiment. The soil in each pot was hand-sorted approximately twice a week and the number of eggs laid and dead beetles were recorded. The leaves were changed three times a week. The experiment continued until all the beetles had died. Data for total eggs and female survival time were analysed using ANOVA for a completely randomized design. Because time intervals between egg counts were not all equally spaced, the data on egg production over time were analysed as egg production rate (eggs per female per day) in a completely randomized repeated-measures ANOVA with the protected LSD test, after data transformation using the $\sqrt{(x+1/2)}$ transformation. Initial female weight was a significant covariate in this analysis ($F_{1,44} = 4.21$, $P < 0.05$).

Results

District survey

Heteronyx piceus larvae were found in 90% of the 28 South Burnett peanut fields surveyed and were the predominant white grub species, averaging 66% of all larvae collected. While *H. piceus* was present in all landscape positions, the distribution of *H. piceus* larval densities varied markedly with the sites' landscape position (fig. 1). Specifically, while all landscape positions had close to 50% of sites in the lowest larval density class (0–0.99 larvae per row-metre), sites in the lower half of the slope were unlikely to have more than moderate populations. Conversely, all the high *H. piceus* larval populations were in the upper half of the landscape, with the highest populations (>12 larvae per row-metre) in the areas classified as plateau, hillcrest and upper hill slopes.

The distribution of crops with more than 4 larvae per row-metre quantifies the degree of this concentration of crop losses in the upper landscape positions. Crops in the lower half of the landscape ('forest' soils) had a 5% probability of exceeding 4 larvae per row-metre (1 site out of 20 over 2 years), compared to 25% for the upper half of the landscape ('scrub' soils) (9 sites out of 36 over 2 years) (maximum-likelihood chi-square = 4.12, df = 1, $P < 0.05$). In summary, the district-wide survey showed that while *H. piceus* occurs in peanut-production soils throughout the district, almost all of

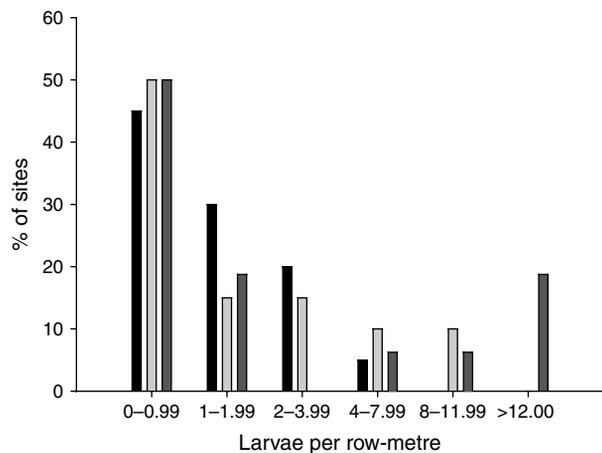


Fig. 1. Distribution of *Heteronyx piceus* larval densities by landscape position (■, Pediment, lower-mid slope ($n=20$); □, mid-upper slope ($n=20$); ▒, plateau, hillcrest, upper hill slope ($n=16$)).

the damaging infestations are found in the 'scrub' soils in the upper landscape positions, with the 'forest' soils in the lower slopes much less likely to harbour high larval populations.

Population dynamics

Eggs were present in the field between early December and early February. This matches the period over which field-collected females laid eggs in the laboratory when fed peanut leaves (fig. 4). *Heteronyx piceus* adults were present during November, December and January in each of the 3 years, reflecting previous observations (Rogers & Brier, 1992).

Each summer, white grub populations increased during December–January to peak in February–March (fig. 2). The pairs of sites with the same crop rotation (table 1) showed the same patterns of larval incidence. Consequently, only data for one of each rotation pattern (fields 2 and 3) are shown in fig. 2a. There was a markedly greater increase during summer in larval populations under peanuts (peak densities: 0.9–1.5 larvae per sample (=3–12 larvae per row-metre)) than maize (peak densities: 0.15–0.45 larvae per sample (=0.5–1.5 larvae per row-metre)). In each cropping season, larval numbers under peanuts were significantly greater than under maize on multiple sampling dates (fig. 2a) ($P < 0.05$). During the main larval occurrence period, *H. piceus* contributed 75% of all white grubs collected. The proportion of larvae that were *H. piceus* was slightly higher and more consistent on peanuts (78.5%; range 63.6–91.3%, $n=8$) than on maize (67.3%; range 4.8–93.9%, $n=8$).

In summary, the sampling in the five fields at the Tingoora study site found that both the absolute numbers of white grubs and the proportion that were *H. piceus* were markedly greater under peanuts than under maize. These data confirm the primary importance of *H. piceus* as a peanut pest. Data published elsewhere (Rogers *et al.*, in press) documents the yield losses that occur from this species in peanuts.

The response of the white grub populations in field 4 (fig. 2b) provides important insights into the population

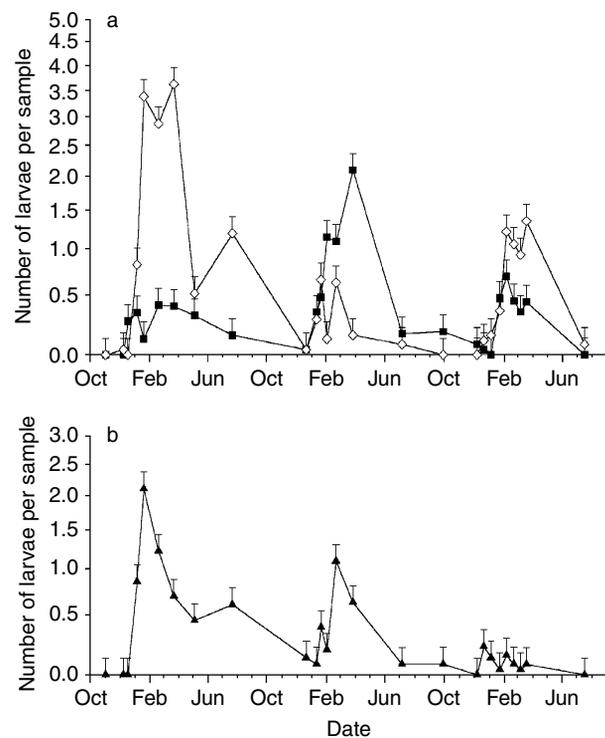


Fig. 2. Total white grub populations over three cropping seasons (November 1998–July 2001). (a) Field 2 (■) (maize–peanuts–maize) and Field 3 (◇) (peanuts–maize–peanuts), (b) Field 4 (▲) (pasture–peanuts–maize). Growth periods: peanut November to April; maize December to June; wheat May to November; approximately. Data transformed by $\sqrt{(x+1/2)}$ prior to analysis, equivalent means (with SE bars) presented.

dynamics of *H. piceus*. Field 4 had been under a peanut–maize rotation for decades until 1996, when a Rhodes grass pasture was sown. Total white grub populations peaked at 2.1 larvae per sample (7.0 larvae per row-metre equivalent) under the pasture in the first year of sampling (the third year of pasture). *Heteronyx piceus* comprised only 13.2% of larvae, or approximately 1 larva per row-metre equivalent, i.e. *H. piceus* persisted under the pasture at densities equivalent to those under maize in the same year in adjacent fields. In year 2 of the sampling, under peanuts, *H. piceus* comprised almost two-thirds of a population that reached 1.08 larvae per sample (3.6 larvae per row-metre), but declined to only 16.7% of a population that peaked at only 0.22 larvae per sample (0.72 larvae per row-metre), under maize in year 3. This sampling confirms that *H. piceus* can persist under pasture, as part of a broader white grub fauna, but can revert to predominating under peanuts at damaging densities after a single season.

Heteronyx piceus adult movement across crop interfaces

The 1999/2000 adult female trapping data indicated that there were no significant effects ($P > 0.05$) for any source that includes distance (i.e. main effect, or two- or three-way interactions) (fig. 3a). This provides clear evidence that there is no detectable migration of females over crop interfaces, i.e. from maize to peanuts, in 1999/2000. There were almost

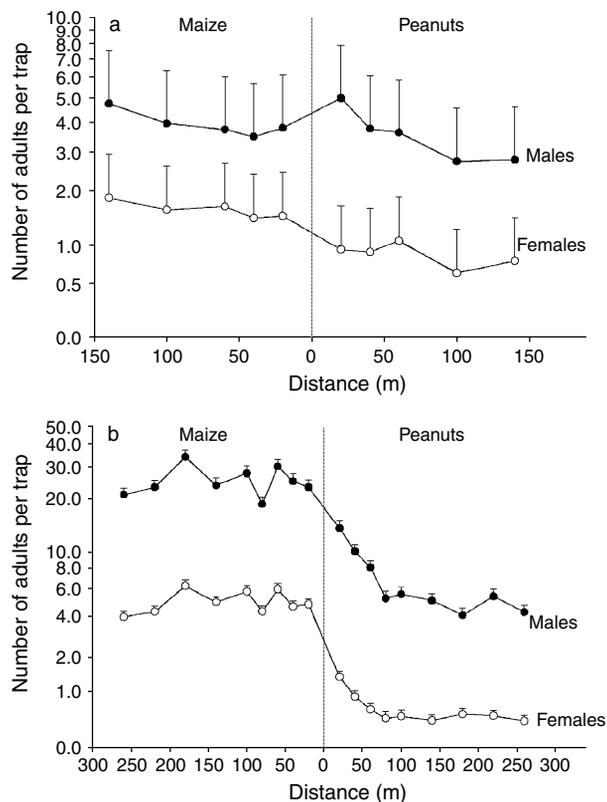


Fig. 3. Catches of *Heteronyx piceus* males (●) and females (○) in interception traps across maize and peanuts during (a) the 1999/2000 and (b) 2000/2001 seasons. Data transformed by $\log_{10}(x+1)$ prior to analysis, equivalent means (with SE bars) presented.

twice as many females caught in traps in maize (1.62 females per trap) in field 3 than the peanuts in field 2 (0.85 females per trap) ($F_{1,356} = 51.24$, $P < 0.001$), reflecting the greater density of larvae under peanuts in field 3 than under maize in field 2 at the end of the previous season (fig. 2a). For males, there were no differences between distances in the maize field, but for peanuts the trap catches at 20 m were significantly greater than for 100 m and 140 m. This indicates that some movement by males occurred from maize to peanuts, but only for short distances, relative to field size. In addition, many fewer females than males were found in interception traps, suggesting that females of *H. piceus* are much less active dispersers than males.

In 2000/2001 there was a significant crop \times distance interaction for both sexes (fig. 3b), indicating that beetles did move across crop interfaces into the peanuts in that year. However, this movement into the peanuts was only to about 40 m from the crop interface for females, and 80 m for males. Compared to the paddock size, this degree of movement is not likely to have a major impact on overall population densities, and was not evident in the end-of-season larval numbers (see below). In maize, numbers of both sexes (males: 24.82 per trap; females: 4.93 per trap) were much higher than in peanuts (males: 6.34 per trap; females: 0.59 per trap) and showed significant spatial variation across the paddock, but not in relation to distance from the crop

Table 2. Total fecundity and survival time for *Heteronyx piceus* adults fed leaves of different food plants.

Adult food	Total eggs per female	Adult survival (days)
Peanuts	56.1 a	68.0 a
Soybean	25.1 b	49.8 b
Sorghum	10.4 c	34.0 cd
Maize	9.8 c	29.4 d
Control (no food)	8.2 c	41.4 bc

Means followed by the same letter are not significantly different (protected LSD test, $P < 0.05$).

interface. As for the previous year, many fewer females than males were found in interception traps.

In the 1999/2000 ANOVA of larval numbers, no sources of variation involving distance (i.e. as main effect or interaction) were significant (all $P > 0.05$), but larval densities in peanuts (2.47 larvae per sample) were almost eight-fold greater than in the adjacent maize (0.32 larvae per sample) ($F_{1,42} = 34.71$, $P < 0.001$). This eight-fold difference in larval density was despite the numbers of female beetles in maize being double those in peanuts at the beginning of the season (fig. 3a).

In 2000/2001 there was no significant crop \times distance effect ($P > 0.05$) for larval numbers, indicating that *H. piceus* larval density in the two crops changed similarly with respect to distance from the crop interface. While there was a significant distance main-effect in 2000/2001 ($F_{21,86} = 2.35$, $P < 0.01$), there was no pattern to the differences with respect to distance from the crop interface. In 2000/2001, larval densities in peanuts (0.95 larvae per sample) were greater than in the adjacent maize (0.29 larvae per sample), despite the numbers of female beetles in maize being eight-fold those in peanuts at the beginning of the season (fig. 3b).

These data on end-of-season larval distributions in fields 2 and 3 over two seasons support the conclusion from the trapping study that migration of females between fields is, at most, very limited and restricted to small distances, relative to field size. It also points to differential reproduction rates in the two crop types, as the ratio of the larval density at the season's end to the female trap catch at the season's start are markedly different in maize and peanuts (0.05883 vs. 1.6102).

Adult food and fecundity

The total number of eggs laid per female was strongly influenced by the food available (table 2). Peanut leaves were by far the best food for egg production, and more than twice as good as the next best, soybean leaves. Maize and sorghum, were poor adult foods for egg production, and were no different to the control (i.e. no food). These results confirm the results of an earlier small-scale study (Rogers, 1989) that compared egg production with and without peanut foliage.

From the perspective of the present study, it is important to note that egg production on peanuts was nearly six times that on maize. Adult survival times parallel the differences in total fecundity (table 2), with adults fed peanut leaves having the longest (68.0 days) survival times ($P < 0.05$). Survival time on maize (29.4 days) was significantly less than

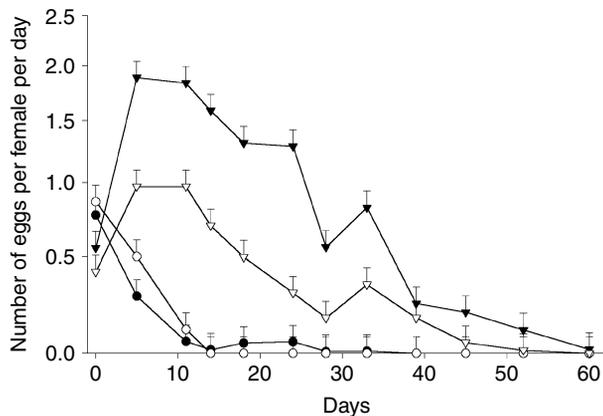


Fig. 4. Egg production rate of *Heteronyx piceus* females on three plant foods and an unfed control. Data transformed by $\sqrt{(x+1/2)}$ prior to analysis, equivalent means (with SE bars) presented. Data for sorghum not shown for presentation clarity: See text for details. ●, Control; ○, maize; ▼, peanut; ▽, soybean.

in the no-food control (41.4 days), suggesting that maize had an actively detrimental effect on the adults.

The analysis of the egg production-rate data produced clear evidence of the difference in suitability of legume and grassy adult food plants (fig. 4). The two crop types produced two different patterns of egg production. Maize and sorghum produced almost identical patterns and showed a consistent decline from the beginning of the experiment with egg-laying almost finished within 21 days. Females laid 8–10 eggs each over the first week, then almost no more until death. This pattern of oviposition was the same as the unfed control ($P > 0.05$), giving clear evidence of the unsuitability of these monocotyledonous crops for *H. piceus* egg production. In contrast, peanuts and soybeans showed an increase in egg production from the beginning of the experiment, to peak between days 12 and 18, then followed by a slow decline over the next six weeks. However, egg production rate for peanuts was about twice that for soybeans throughout. There was no difference between egg production rate in beetles fed maize and peanuts up to the first sampling date, but it was greater in beetles fed peanuts than in those fed maize ($P < 0.05$) for all subsequent dates. In maize, no eggs were laid after day 18.

Discussion

District survey

The characteristics of the soils derived from deeply weathered basalt vary with landscape position, with soil pH being the most obvious (Sorby & Reid, 2001). The 'forest' soils in the lower slope positions have soil surface pH of medium to slightly acid (5.9–6.4) with neutral to alkaline subsoils. The 'scrub' soils higher up the slope are very strongly to slightly acid (4.6–6.5), with extremely to medium acid subsoils (Sorby & Reid, 2001). However, these soil pH differences do not appear to be the likely cause of the differences in infestation risk recorded. The available data on the impact of soil pH on scarab oviposition (Vittum & Murzuch, 1990; Cherry & Allsopp, 1991) and larval survival (Vittum & Tashiro, 1980; Cherry & Allsopp, 1991) show no

impacts from soil pH over approximately 3 pH units for four species of adults and five species of larvae. Consequently, while there is a clear association between soil type and infestation risk by *H. piceus* on the South Burnett soils derived from weathered basalt that has value for management of the pest, the reason for this association is unclear.

Adult food and fecundity

Robertson *et al.* (1999) concluded that none of the three major scarab species they reviewed – *Costelytra zealandica* (White), *Dermolepida albohirtum* (Waterhouse) and *Phyllophaga horticola* (Linnaeus) – had upper population limits set by the quality of adult food. In *P. horticola*, adult feeding had no effect on fecundity (Milne & Laughlin, 1956). While Farrell (1973) found the *C. zealandica* fecundity was increased by feeding (from 11.1 to 17.9 eggs per female), overall population trends were determined through summer drought, insecticide application or cultivation disrupting pathogen-mediated oscillations (Popay, 1992; Robertson *et al.*, 1999). *Dermolepida albohirtum* population cycles were linked to the effects of highly virulent non-persistent diseases (Robertson *et al.*, 1997b) rather than adult food. In another scarab species, *Sericesthis geminata* Boisduval, Wensler (1971) found that females showed a similar response to *C. zealandica*, with an increase from 14.5 to 27.5 progeny per female in response to adult feeding. However, all these species exhibited at best a moderate increase in fecundity in response to feeding, compared to *H. piceus*, which increased fecundity nearly seven-fold when fed peanut foliage.

Two of the existing reports of marked adult-food effects involve white grubs from the tribe Heteronycini, the same melolonthinid tribe as *H. piceus*. Robertson & Kettle (1994) reported that an undescribed *Pseudoheteronyx* species in central Queensland laid 18.5 eggs when fed sunflower, but only 3.0 eggs per female when fed the weed *Parthenium hysterophorus*. Morgan *et al.* (1978) found that *Heteronyx obesa* Burmeister adults that had fed on sorrel (*Rumex* spp.) laid significantly more eggs (6.1 eggs over one week) than those fed on geranium (3.1 eggs) or grass (1.1 eggs). This strong positive response of fecundity to adult food in these three heteronycinid species suggest that they are representative of an scarab life history strategy that is additional to those considered by Robertson *et al.* (1999).

Management implications

This series of studies into *H. piceus* biology and ecology has clarified key aspects of this species' population ecology in the peanut–maize cropping system in the South Burnett area of Queensland, Australia. Firstly, the previously observed pattern of *H. piceus* occurrence, with a mosaic of high larval populations under peanuts and low populations under adjacent maize, has been formally documented in a long-term intensive study of an infested farm (fig. 2). Furthermore, this study has documented that in any one field, this population mosaic flips from high to low and vice versa as peanuts and maize are grown alternately. Larval populations are markedly higher under peanuts than adjacent maize, reflecting the greater fecundity of females in peanut fields at the beginning of the season (figs 2 and 4). Adult numbers are typically higher in maize fields (fig. 3), reflecting the higher larval numbers in the peanut crop in that field in the previous season.

Secondly, while some adult movement between fields was detected (fig. 3), this effect is not strong enough to cause the documented high larval populations in peanuts and low populations in maize. Thirdly, end-of-season larval distribution within fields of both maize and peanuts are each relatively uniform and do not show detectable edge effects at crop interfaces that would be indicative of adult migration between fields. Thus, the larval distribution data confirm the lack of significant population movement in the adult stage. Finally, the underlying cause of high larval populations in peanut crops is now clear; enhanced fecundity of *H. piceus* feeding on peanut foliage (table 2, fig. 4) is sufficient for low adult populations in peanuts during early summer to lead to high larval populations in peanuts later in the same season.

The laboratory feeding experiments point to soybean as a suitable food crop for *H. piceus* development. This indicates that farming systems containing this crop in the known range of this species could be at risk. However, soybeans may be less damaged by *H. piceus* because seeds do not develop in the ground and the tap root system is stouter than that of peanuts. Additionally, soybeans are unlikely to exacerbate losses on peanuts as they are typically grown on heavier soils than peanuts; consequently the two species do not commonly occur in the same crop-rotation system.

Common approaches to soil pest problems include cultural control and crop rotation (Robertson *et al.*, 1997a). The data on food effects on adult fecundity (fig. 4) indicates that the existing peanut-maize crop rotation already exerts considerable downward pressure on *H. piceus* population growth, compared to cropping systems with more frequent peanut crops. Each time maize is grown, it reduces the reproductive success of the large number of adults that emerge from larvae that developed in the previous peanut crop. Peanuts were grown more frequently in the rotation (e.g. maize-peanuts-peanuts) in the South Burnett region in the 1960s to 1980s, but this is no longer favoured because of the increased incidence of soil-borne diseases and adverse effects on soil physical structure (Crosthwaite, 1994). During that time, high *H. piceus* populations were a feature of the second peanut crop in these maize-peanut-peanut cropping sequences. In the 1999–2000 district-wide survey, two of the sampling sites were double-cropped with peanuts; both of these sites had moderate to high populations in both years, confirming consecutive peanut crops as a risk factor, as noted previously by Rogers & Brier (1992). The studies at the Tingoorra site clarify the reason for this – the large number of adults emerging after the first peanut crop each produced large numbers of eggs on the succeeding peanut crop, leading to very high larval densities in the second peanut crop.

The data presented here indicate that females are relatively sedentary, and are unlikely to move much beyond the field boundary within which they emerge. This difference between sexes in behaviour is known to occur for other scarabs, e.g. *Antitrogus parvulus* Britton (Coleoptera: Scarabaeidae) (Logan, 1997), and can be important in determining appropriate management strategies. In this case, this lack of mobility of females points to the individual field being the most appropriate management unit for *H. piceus*, rather than the whole farm or district. Additionally, the large fecundity response of females to peanut foliage suggests that tactics protecting a specific season's crop will be more appropriate than longer-term suppression of populations because

damaging larval populations can develop from low adult numbers in peanuts within the course of a single season.

These factors point to treatments that target either adults before they have laid eggs, or larvae in the soil before they are large enough to damage pods. The former option has been attempted (D.J. Rogers, unpublished data) but has logistical difficulties that make it impractical commercially. At this stage, treatments targeting young *H. piceus* larvae appear to be the management option with the greatest potential for success, with the most obvious options being in-furrow or seed-dressing treatments, applied at planting. However for commercial success, a mechanism for identifying at-risk fields prior to planting would be important as this would enable more rational and economic decisions to be made regarding their application. Landscape position/soil type provides one key factor on which to assess a site's risk; peanuts planted on 'scrub' soils (in the upper half of the landscape) are much more at risk of infestation than crops planted on 'forest' soils in the lower half of the landscape.

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