DRAFT ASSESSMENT REPORT

1. Provide information on the taxonomy of the species

The following information is required about the taxonomy of the species and its role in its natural environment:

a) Family name: Gryllidae

b) Genus name: Gryllodes

c) Species: sigillatus

d) Subspecies: There are no known subspecies for *Gryllodes sigillatus*. However, for many decades *Gryllodes sigillatus* was often incorrectly named as *Gryllodes supplicans*. *G. sigillatus* and *G. supplicans* are now known as two distinct species (see attached reference by Otte, 2006)

e) Taxonomic Reference:

Otte, D & Alexander, RD (1983) *The Australian Crickets (Orthoptera: Gryllidae)*. Monograph 22, Academy of Philadelphia, Allen Press, Kansas. Pages 160 – 162, Illustrations (page 161, Figures 119 and 120).

Otte, D (2006) *Gryllodes sigillatus* (Walker) is a valid species distinct from *Gryllodes supplicans* (Walker). *Transactions of the American Entomological Society*, 132: 223-227.

f) Common Names: *Gryllodes sigillatus* is known by various common names worldwide, including: decorated cricket, tropical house cricket, Indian house cricket, banded cricket.

g) Is the species a genetically-modified organism (GMO)?

This is *not* a genetically-modified organism.

2. Provide information on the status of the species under CITES

***The Convention on International Trade in Endangered Species of Wild Fauna and Flora* (CITES) is an international treaty involving over 150 countries with the purpose of protecting wildlife from unregulated trade. Australia, as a member country, controls the import and export of species that are threatened or could become threatened due to trade in them or their products.**

A species may be affected in its natural environment by factors such as habitat destruction and fragmentation, and illegal collection for a variety of purposes e.g. for the pet industry. To help mitigate the threat of collection and trade, the species could be listed in the CITES Appendices. A species on CITES Appendix I or II requires appropriate CITES import permits to enter Australia.

If the proposed species for import is listed on CITES Appendix I or II, discuss as appropriate:

- **implications of illegal trade**
- **popularity of the species in trade e.g. pet industry**
- **status of the species in its natural range e.g. threatened, endangered, protected etc.**
- **reason the species is threatened.**

CITES listing is taken into account when considering restrictions in countries outside the species' natural range.

Gryllodes sigillatus is *not* listed on CITES Appendix I or II.

3. Provide information about the ecology of the species

These characteristics may influence the likelihood of the species to establish feral populations:

a) Longevity: what is the average lifespan of the species in the wild and in captivity?

I have shown in my own research that the average lifespan of adult male *G. sigillatus* in captivity is 73.62 days, whereas the average lifespan of adult females is much shorter at 50.42 (Archer *et al.* 2012). No attempt has been made to estimate the lifespan of *G. sigillatus* in the wild. However, work on other cricket species suggests that *G. sigillatus* is extremely unlikely to live as long in the wild as in captivity. In the European field cricket *Gryllus campestris*, 24 hours a day video recording of crickets during the breeding season in Spain showed that males of this species live on average 23.2 days and females an average of 25.8 days (Rodriguez-Munoz *et al*. 2010). In Australia, a large-scale mark and release experiment in the wild on the native black field cricket *Teleogryllus commodus* estimated average male lifespan at 15.2 days and female lifespan at 21.4 days (Zajitschek *et al.* 2009). The reduced lifespan of adults in the wild compared to captivity is likely to reflect predation (see below) and the more extreme climatic conditions experienced.

b) What is the maximum length and weight that the species attains? Provide information on the size and weight range for males and females of the species.

Females are, on average, larger than males in *G. sigillatus*. From my own data, adult females range in length from 12.1 to 22.2 mm (excluding hind legs and the ovipositor – see Figure 1 below), in weight from 125.9 to 399.20 mg and in pronotum width from 2.80 to 5.50 mm. Adult males range in length from 14.2 to 18.3 mm (excluding hind legs), in weight from 105.50 – 316.10mg and in pronotum width from 2.35 to 5.25 mm.

c) Discuss the identification of the individuals in this species, including if the sexes of the species are readily distinguishable, and if the species is difficult to distinguish from other species.

Where possible provide representative photographs of female and male specimens at all life stages. Ensure you have appropriate copyright permission as the report will be published on the Department's website.

Gryllodes sigillatus is a small (12.1 to 22.2 mm in length), light yellowish-brown cricket that is dorsoventrally flattened (compressed in thickness). It is therefore easily distinguished from most Australian field crickets that are larger (>25 mm in length), much darker in colour (dark brown to black) and are not dorsoventrally flattened. The cricket most similar in appearance to *G. sigillatus* in Australia is the introduced house cricket *Acheta domesticus*. Both species are light brown in colour and similar in size. However, the two species can be easily distinguished by the fact that (1) *A. domesticus* is not dorsoventrally flattened; (2) the space between antennae is narrower in *G. sigillatus* (about the width of the basal segment of either antenna) than *A. domesticus* and (3) there is a single black transverse line between the eyes in *G. sigillatus* but not in *A. domesticus*. The acoustic signal of male *G. sigillatus* is also very distinct from other Australian crickets, including the introduced *A. domesticus*. The calling song consists of a sequence of brief chirps, with each chirp having three principal pulses, and the dominant frequency of the call is 6.2 kHz. This is noticeably higher than the frequency of all other field crickets in Australia which range between 3 and 5 kHz (Otte & Alexander 1983). A spectrogram and an acoustic sample of the male call can be found at: http://entnemdept.ifas.ufl.edu/walker/Buzz/501a.htm.

The sexes in *G. sigillatus* cannot be distinguished for the first 5 larval instars (Figure 1A-E). At the 6th larval instar (Figure 1F), males and females can be separated by the growth of the ovipositor bud in females. This sex difference (and ovipositor bud) becomes more pronounced in 7th instar larvae (Figure 1G). The sexes are easily distinguished as adults: all males have short wings used for acoustic signalling that cover half of the abdomen whereas females are wingless, and females have a fully functioning ovipositor (used to lay eggs into the soil) whereas males do not (Figure 1H). The pictures provided in Figure 1 are taken from my own stock cultures of *G. sigillatus* and therefore I hold the appropriate copyright permission. I am willing for this figure to appear on the Department's website.

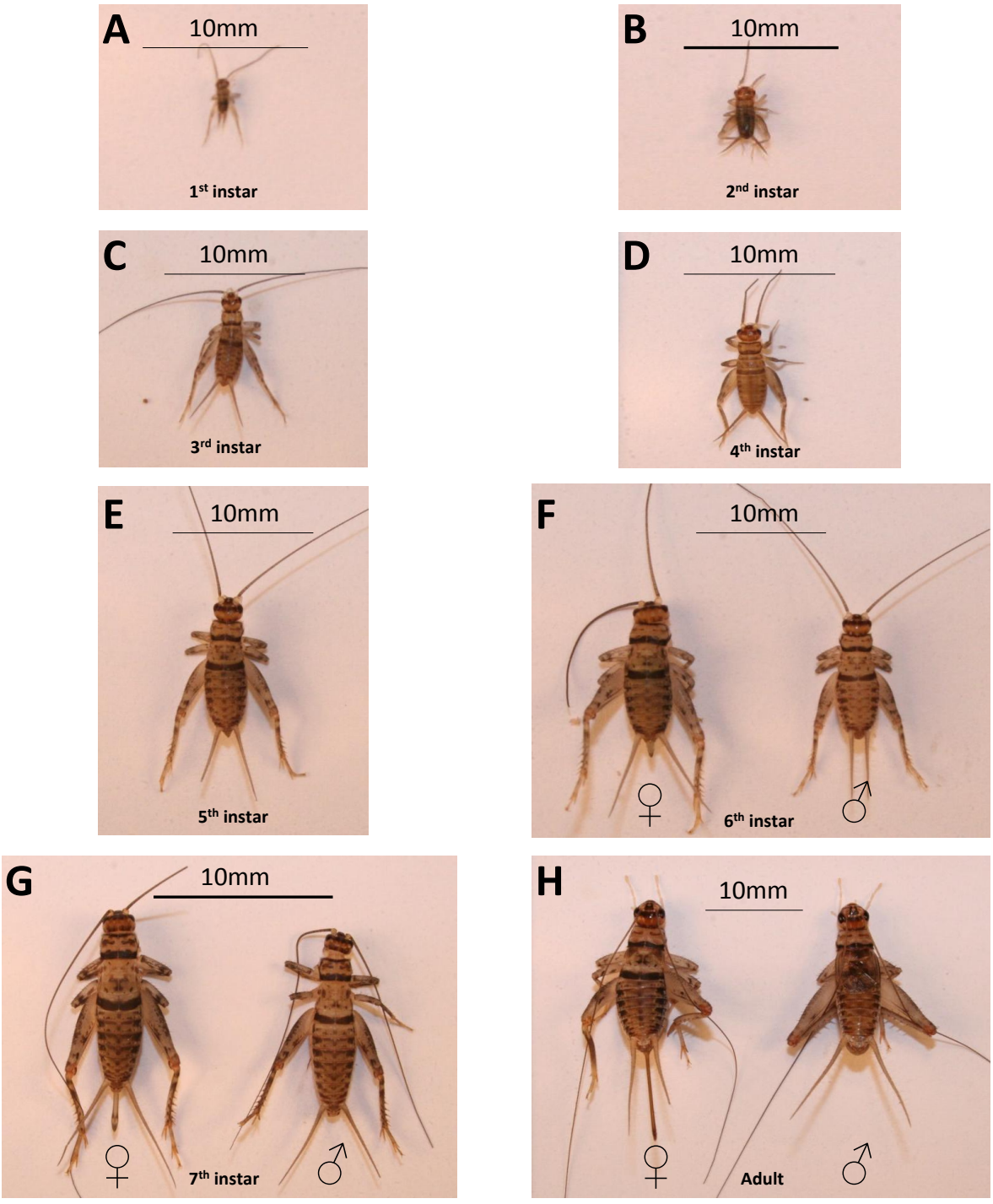

Figure 1. The development stages in *Gryllodes sigillatus*. The sexes cannot be distinguished in the first five larval instars (A-E). In the 6th instar, females start to develop an ovipositor bud that can be used to separate the sexes (F) and this becomes more pronounced in 7th instar larvae (G). At adulthood (H), males and females are easily separated: males have wings for calling and females have a functional ovipositor for laying eggs into the soil.

d) Natural geographic range. What is the country of origin and what is the natural distribution of this species? Where does the species occur naturally? Exclude any areas where the species has been introduced through human intervention. Describe any population limiting influences in its natural range including: predator/prey relationships, competition, availability of resources etc.

Very little is known about the natural geographical range of *G. sigillatus*. Most researchers believe that this species is likely to be native to either Southern Asia (e.g. India, Pakistan and Sri Lanka) or Southwestern Asia (e.g. Saudi Arabia, Turkey, Syria, Cyprus) or both. Part of the difficulty in determining that natural geographical range of *G. sigillatus* is that this species now has a world-wide distribution (see below).

Very little is also known about the factors that limit the population size of *G. sigillatus*, especially in their natural range. Studies on laboratory populations of *G. sigillatus*, however, do suggest a number of factors that may limit the natural range of this species:

(i) The sexually transmitted nematode (*Mehdinema alii*) is known to target male *G. sigillatus*, whereas female *G. sigillatus* serve only as vectors for nematode transmission (Luong & Kaya 2005). Although this nematode causes only low mortality in males it does reduce the size of the spermatophylax. Thus, it is possible that *M. alii* will have a deleterious effect on reproduction in *G. sigillatus* that may limit numbers.
(ii) The insectivorous mediterranean house gecko (*Hemidactylus tursicus*) orients and predates calling male *G. sigillatus*, as well as females that are responding to these calls (Sakaluk & Belwood 1984). Other species of field crickets have been shown to be predated by a range of different predators, including bats (Bailey & Haythornthwaite 1998), birds (Rodriguez-Munoz *et al*. 2011), domestic cats (Walker 1964), small mammals (e.g. shrews, Rodriguez-Munoz *et al*. 2011), spiders (Rodriguez-Munoz *et al*. 2011), parasitiods (Wagner 1996) and assassin bugs (Rodriguez-Munoz *et al*. 2011). It is likely that many of these predators also target *G. sigillatus* in their natural range.
(iii) When deprived of food, but given unlimited access to water, *G. sigillatus* can typically live for about 2 weeks, but when deprived of food and water they rarely live more than 48 hours (Burpee & Sakaluk 1993). Thus, an available supply of food and especially water appears key to limiting the natural distribution of this species. It also explains the strong affinity of *G. sigillatus* to human dwellings and tropical climates, where food and water are in abundance.

e) Is the species migratory? Identify if the species moves seasonally between different habitats. Migratory behaviour may occur between countries, within one country, or may occur on a small scale, for example from high altitudes to low altitudes on a mountain range.

G. sigillatus is *not* migratory.

f) Does the species have the ability to hibernate in winter or aestivate (go into stasis or torpor) in the summer months)?

No, *G. sigillatus* is generally restricted to warmer tropical climates where it breeds continuously throughout the year. Development time is temperature-dependent so that growth is likely to be slower over the winter period.

g) Does the species have the ability to breathe atmospheric air i.e. has accessory breathing organs? (fish and other mobile aquatic animals)

Not applicable.

h) Outline the habitat requirements for all life stages of the species:

- **physical parameters (e.g. salinity, oxygen, pH, temperature) of the natural habitat;**

All life stages of *G. sigillatus* require an abundant supply of food and water, as well as shelter for protection. Adult females also need moist sand and/or leaf litter for reproduction and they oviposit eggs directly into this substrate.

- **climate;**

G. sigillatus requires a warm, tropical climate. Indeed, it occupies such habitats in its world-wide distribution, including Australia. This climate allows *G. sigillatus* to breed continuously, although reproduction and development is likely to be slowed with a reduction in temperature.

- **What nest sites can the species use? 'Nest' is taken to mean a specific area individuals return to in order to sleep, bear or rear young. Identify where the species does/can nest. For example tree hollows; burrows; caves; buildings; cliff faces; dams, lake, pond marsh, swamp, reed-bed; particular ground surface; particular vegetation type; other (specify).**

G. sigillatus do not use specific nesting sites *per se*. They take shelter (i.e. hide and rest) in the crevices and cracks between pavement blocks surrounding buildings. However, both sexes leave these areas at night to forage and mate, and females oviposit in surrounding soil and leaf litter. At times, they can enter human dwelling and take up residence under domestic appliances or furniture but they cannot reproduce in this environment. Occasionally, *G. sigillatus* can be found away from human habitats, occurring in rocky road-cuts and hillsides, but this is less common (Otte & Alexander 1983)

- **Does the species nest, shelter or feed in or around any of the following habitats? Marshes or swamps; estuaries, lakes, ponds or dams, rivers, channels or streams, banks of water bodies; coastal beaches or sand dunes (specify). This question seeks to identify if the species could impact on habitat(s) listed.**

G. sigillatus does not nest, shelter or feed in any of the above habitats. It largely occupies urban areas, especially around human dwellings (i.e. crevices in brickwork and between pavement blocks, under refrigerators).

i) Social behaviour or groupings. Describe how the animal would naturally dwell, for example in social groups, pairs, solitary; animals may be predominantly solitary except during breeding seasons etc. How does the species behave towards its own kind and other species?

In wild populations, male *G. sigillatus* space, on average, 4 meters apart (Sakaluk 1987). This pattern is common among field crickets and males use their acoustic calls to regulate this spacing behaviour to ensure minimum interference when attracting females. Consequently, they are largely solitary except for when mating. However, when shelter is in abundance, *G. sigillatus* has also been observed to naturally group, especially females (Sakaluk 1987). These groupings are dynamic, however, with individuals moving regularly between shelters: this grouping is therefore unlikely to be social but instead based on the excess of a shelter resource (Sakaluk 1987). *G. sigillatus* has not been observed grouping with other species.

j) Is this species ever territorial or does it exhibit aggressive behaviour? Is the species naturally territorial? If so, what would the natural territory range be? Identify whether this species has ever acted in an aggressive manner towards other species, including humans, outside of any usual predator-prey interactions.

Relative to other field crickets, *G. sigillatus* shows a *low* level of territoriality. As mentioned above, males use acoustic signals to space themselves through the habitat to avoid aggressive interactions. *G. sigillatus* does not act aggressively to other species, including humans.

k) Characteristics that may cause harm to humans or any other species. Is the animal capable of inflicting harm? A response for this question would arise if the species has organs such as teeth, a bill, spines or claws that are capable of causing injuries to people that are more significant than minor cuts or bruises.

G. sigillatus does not have any characteristics that are capable of causing harm to humans or other species.

4. Provide information on the reproductive biology of the species

Assess and describe the reproductive characteristics of the species

a) At what age does this species reach sexual maturity (males and females)?

Male *G. sigillatus* commence producing an acoustic signal to attract a mate and are able to produce viable offspring at 6 days post-eclosion to adulthood. Female *G. sigillatus* are also willing to mate and produce viable offspring at 6 days post-eclosion to adulthood. This

information is based on laboratory experiments where crickets have been fed an optimal diet and are maintained at an optimal temperature (32°C). Consequently, it is possible that sexual maturity may be longer than under more extreme, natural conditions.

b) Discuss the species' ability to reproduce; triggers for breeding; breeding site requirements.

G. sigillatus does *not* undergo diapause and therefore breeds continuously at optimized conditions (32°C, abundant food, water and shelter). Little is known about the triggers for breeding in this species, although it is likely that daily temperature and day length play an important role. In Australia, *G. sigillatus* breeds more in summer and spring than in autumn and winter. Females require a moist substrate to breed (soil, leaf litter), as they directly oviposit eggs into this substrate.

c) How frequently does breeding occur?

G. sigillatus does *not* diapause and breeds continuously as an adult, as long as the appropriate conditions exist (32°C, abundant food, water and shelter). Given that reproduction is temperature-dependent in *G. sigillatus*, it is likely that the frequency of breeding is reduced over colder months.

d) For sessile aquatic invertebrates include details of:

- **the length of time spent as motile larvae or plankton**

Not applicable.

- **growth patterns (e.g. is it colonial or does it grow as a solitary animal) characteristics or behaviour that enable the species to survive drought, or other adverse conditions (e.g. forming cysts or spores).**

Not applicable.

e) Can individuals of the species change sex? (reptiles, amphibians, fish and other mobile aquatic animals)

No, *G. sigillatus* remains the same sex through its lifetime.

f) Ability of the species to hybridise. Describe any known crosses. Are progeny of such crosses fertile?

G. sigillatus is *not* known to hybridize with other cricket species.

g) Could the species hybridise with any Australian native species? Identify whether the species could negatively impact native species through hybridisation (cross-breeding with native species).

It is extremely unlikely that *G. sigillatus* could hybridize with any Australian native cricket species. According to Otte & Alexander (1983), *G. sigillatus* is the only species in the *Gryllodes* genus in Australia (i.e. there are no native members of this genus in Australia). As most hybridization in field crickets occurs between species in the same genus, it is therefore unlikely that *G. sigillatus* would hybridize in Australia. A very recent molecular phylogeny of field crickets (Chintaun-Marqier *et al.* 2016) suggests that the most closely related species to *G. sigillatus* (present in Clade G4 in Figure 6 of Chintaun-Marqier *et al.* 2016), and therefore the most likely to mate and create hybrids, all occur in either Southern Asia or Africa. None of these species are native to Australia.

h) Are individuals single sexed? (i.e. either male or female) or hermaphroditic (i.e. have both male and female reproductive organs)

G. sigillatus is single sexed.

5. Provide information on whether this species has established feral populations

a) Has this species ever established a breeding population outside of its native range? Identify any areas where this species has established a breeding population outside of its natural range.

Yes, *G. sigillatus* has established breeding populations world-wide. Although a formal survey of the distribution of *G. sigillatus* does not exist, Otte & Alexander (1983) have identified or collected this species in the United State of America, Brazil, Africa, Australia and Hawaii. Given that this reference is now over 30 years old, the number of countries where *G. sigillatus* has established breeding populations is likely to be much larger than this.

b) Is the species considered a pest anywhere in its natural or introduced range? A pest is a species of animal that causes wide-scale economic cost or amenity loss through its presence or activities. Identify whether this species is subject to active management to reduce population numbers.

G. sigillatus is not considered a pest anywhere in its natural or introduced range. They typically do not harm to humans or other animals and established populations are not actively managed to reduce population numbers. On occasion, they can enter human dwellings and will reside under domestic equipment (e.g. refrigerators) or furniture (e.g. sofas). In these instances, males can call from these locations and become a “nuisance pest” (i.e. causes minor annoyance but does not represent a major threat). They can be easily eliminated, however, using commercial cockroach baits or surface spray insecticides (e.g. Baygon Crawling insect spray).

c) Has the species been introduced to other countries, even if it has not established feral populations?

Yes, *G. sigillatus* has been introduced to a large number of countries world-wide. Established feral populations have been documented in United State of America, Brazil, Africa, Australia and Hawaii (Otte & Alexander 1983). In addition, this species has also been introduced extensively through the United States of America and Europe as a live food for pets (usually reptiles). Although feral populations in the wild have not been established in these countries due to the cold climate (the exception being Florida in southern USA), it is common to be able to purchase *G. sigillatus* in commercial pet stores.

6. Environmental risk assessments of the species

Have any risk assessments of the species, or similar species been carried out in Australia or overseas? Include the results of those assessments in the report.

No risk assessments for the introduction of *G. sigillatus* have been carried out in Australia or overseas. The Pacific field cricket (*Teleogryllus oceanicus*) is currently on the "List of Specimens taken to be Suitable for Live Import" list so presumably has undergone risk assessment in Australia, but I am unable to locate this document on the Australian Government (Department of the Environment) website. The conditions for the import of *T. oceanicus* is "*Eligible non-commercial purpose only, excluding household pets. High security facilities only*".

7. Assess the likelihood that the species could establish a breeding population in Australia

The following points outline the information required for determining the likelihood that the species could establish and inhabit possible matches in the Australian environment.

a) Ability to find food sources. Is the species a generalist feeder or does it have specific food needs? What is the likelihood of it finding food in Australia if it was released or escaped? Describe the feeding characteristics of the species, including whether it has a similar diet to any Australian native species.

G. sigillatus is a generalist feeder and particularly targets human food items around and in dwellings. It is common to find *G. sigillatus* in outdoor paved areas where humans eat meals. Given that breeding populations of *G. sigillatus* already occur in Australia, it is therefore likely that any released or escaped crickets will utilise this food source. Like most native Australian field crickets, *G. sigillatus* feeds at night (i.e. nocturnal feeder) and will consume grass and scavenge dead insects. However, it is unlikely that the diet of *G. sigillatus* will overlap completely with Australian native crickets due to the difference in habitats occupied. For example, many Australian native field crickets consume hard seeds and it is unlikely *G. sigillatus* will be able to consume such items due to the smaller and weaker mouthparts.

b) Ability to survive and adapt to climatic conditions. Describe the characteristics or behaviour that would enhance its ability to survive extreme climatic conditions (e.g. drought) and its ability to adapt to different environments.

G. sigillatus is well adapted to tropical and hot environments, as illustrated by the world-wide distribution of this species in such regions. It survives these conditions by co-existing with human habitation which provides an abundance of shelter to escape the heat, as well as an abundant supply of food and especially water (through reticulation). The nocturnal existence of *G. sigillatus* also helps it survive extreme daytime temperatures. *G. sigillatus* is not well adapted to cold climates, which is likely to explain why it has not established breeding populations in countries with low winter temperatures (i.e. UK and Europe).

c) Ability to find shelter. Can the species live in modified habitats? Identify if this species can live in habitats that have been modified by humans, either directly or indirectly, e.g. plantation forests; gardens; orchards; vineyards; crops; cities or towns; buildings; improved pastures; dams, channels or drains; other (please specify).

G. sigillatus easily finds shelter in Australia. It targets habitats modified by humans, especially crevices in brickwork and between pavement blocks. Occasionally, *G. sigillatus* will also enter human dwellings and buildings, taking refuge under domestic appliances (e.g. refrigerators) and furniture (e.g. sofas). *G. sigillatus* is not known to occupy other habitats modified by humans, such as plantation forests, gardens, orchards, vineyards, crops, improved pastures, dams, channels or drains. These habitats are more likely to be utilized by native field crickets.

d) Reproduction. Could factors such as longevity, birth rates and numbers of offspring increase the likelihood of the species to establish?

Reproduction is one of the key features driving the world-wide success of *G. sigillatus*. While the average lifespan of *G. sigillatus* is not markedly longer than other native Australian field crickets (such as *Teleogryllus oceanicus* and *T. commodus*), the fecundity of this species is much higher and the survival of nymphs after hatching from egg is much greater (at least in the laboratory). In captivity, *G. sigillatus* will produce approximately 60 eggs per day with 85% successfully hatching, whereas *T. commodus* will produce approximately 30 eggs with 65% successfully hatching (Hunt, personal data).

e) Are there any limiting influences on the species' natural range? Predator/prey relationships, competition, availability of resources etc. Assess what similar population constraints might exist in Australia.

There are a number of factors that are likely to limit the distribution of *G. sigillatus* in Australia. Although the effect of predation on *G. sigillatus* numbers has not been examined in Australia, it is likely that a myriad of different predators in Australia will be capable of targeting this species. I have personally observed lizards, birds, mammals (e.g. *Antechinus*,

dunnarts, bats) and spiders using the acoustic signal to locate and predate native field crickets in Australia. There are published reports that geckos (Sakaluk & Belwood 1984) and domestic cats (Walker 1964) use a similar strategy to predate *G. sigillatus* in the United State of America. The availability of food and especially water is also likely to be important to limiting the distribution of this *G. sigillatus* in Australia: when deprived of food, but given unlimited access to water, *G. sigillatus* can typically live for about 2 weeks, but when deprived of food and water they rarely live more than 48 hours (Burpee & Sakaluk 1993). Temperature is also likely to limit the distribution of *G. sigillatus* in Australia. Where the range of *G. sigillatus* has expanded around the globe, it has always been in tropical climates (i.e. Florida, Brazil) or warm climates with an abundance of water provided through urbanization (i.e. Perth). It is therefore unlikely that populations would spread into colder areas in Australia (i.e. Victoria or Tasmania). Finally, the availability of shelter and breeding sites is unlikely to be a limiting factor in urbanized areas in Australia (as *G. sigillatus* thrives in such areas) but will limit population expansion in non-urban areas.

f) Address the issue of increased potential for feral population establishment if more individuals of the species were present in Australia.

Large and well-established breeding populations of *G. sigillatus* already exist in warm and tropical climates in Australia (including Perth, Adelaide, Sydney and Brisbane). Clearly the potential exists for *G. sigillatus* to establish additional feral populations in Australia if released, but this should have negligible effects on the overall number of this species in Australia.

8. Provide a comprehensive assessment of the potential impact of the species should it become established in Australia

Summarise the potential impact on the environment of importing the specimen. Address both the potential impacts of the particular import that is proposed, and the potential impacts of the species should the specimen(s) ever be released from effective human control.

It is important that a full explanation and comprehensive analysis, including the costs and benefits, of each aspect is undertaken.

An application will not be continued if information provided in this section is inadequate.

a) Does the species have similar niche/living requirements to native species?

- **Could wild populations of the species use the same resources as native Australian species, for example that it would compete with for food, shelter etc.**

It is extremely unlikely that the resources of *G. sigillatus* and native Australian field crickets will completely overlap. Most native Australian field crickets construct burrows for shelter, feeds on a variety of vegetation (i.e. grass and seeds) and inhabit pastures and scrubland. In

contrast, *G. sigillatus* occupies crevices in brickwork and between pavement blocks, and scavenges for food items in and around human dwellings. Thus, the area of overlap between *G. sigillatus* and native Australian field crickets is likely to be small and this should minimize competition for resources.

- **If 'yes', what types of resources could be used and which types of Australian native species could be affected: food; water; space; rest or shelter sites; nest sites; other. What native species would be affected?**

Not applicable.

- **If the species you are proposing to import is a mammal, identify if it can climb trees.**

Not applicable.

b) Is the species susceptible to, or capable of transmitting any pests or diseases?

Like most field crickets, *G. sigillatus* is susceptible to Cricket Paralysis Virus (CrPV) that already exists in Australia (it was first discovered in the native Australian field crickets, *Teleogryllus oceanicus* and *T. commodus*). *G. sigillatus* is also susceptible to the recently identified *Acheta domesticus* densovirus (AdDNV) that has devastated the cricket pet food industry in the United States of America (Weissman *et al.* 2012). However, AdDNV infects but does not kill *G. sigillatus*. Given the general lack of niche overlap of *G. sigillatus* and native Australian field crickets, it is unlikely that these diseases would be successfully transmitted. Most importantly, the stocks of *G. sigillatus* I wish to import to Australia have been captive bred for the last 24 generations (~3 years) and are free from the above diseases.

c) Probable prey/food sources

- **Does the species attack or prey on wildlife? Identify if the species has the capacity to attack or prey on wildlife. If 'yes', specify whether the prey are: waders or waterfowl; other birds; mammals < 1 kg; mammals 1–5 kg mammals > 5 kg; amphibians; vertebrate eggs; fish; aquatic invertebrates; reptiles; insects; land invertebrates; other; (specify).**

No, *G. sigillatus* does not attack or prey on wildlife.

- **Does the species attack or prey on domestic or commercial animals or plants?**

No, *G. sigillatus* does not attack or prey on domestic or commercial animals or plants.

d) Impacts on habitat and local environments.

- **Could the species reduce the ground vegetation cover to an extent where it could cause or increase soil erosion? This question looks at identifying if the species, through**

feeding, digging or other activities could have a detrimental impact on vegetation such that the underlying soil is exposed to increased erosion.

Unlike many native Australian field crickets (e.g. *Teleogryllus commodus* that is considered a pasture pest), *G. sigillatus* does not dig burrows or feed on pastures or other economically important vegetation. *G. sigillatus* exists almost exclusively around human habitation, residing in the crevices in brickwork and between pavement blocks, and is therefore likely to have little effect on natural ground vegetation and soil erosion.

- **Does the species construct burrows or dig near or around waterways? Identify if the species does/can burrow or otherwise disturb the substrate (soil or sand) around waterways.**

G. sigillatus does *not* dig burrows near or around waterways. It resides in the crevices in brickwork and between pavement blocks associated with human habitation.

- **Has the species ever been recorded causing damage to: native animals' habitats; natural communities; native plants; forestry; agriculture?**

G. sigillatus has never been recorded causing damage to native animal's habitats, natural communities, native plants, forestry or agriculture.

- **Could the species inhibit tree seedling regeneration in forests and woodland? This question aims to identify if the species could have a negative impact on regeneration in native forests and woodlands.**

No, *G. sigillatus* coexists with human habitation and has never been observed in native forests or woodlands. Thus, this species is unlikely to negatively impact seedling regeneration.

- **Could the species spread weeds? Identify whether the species could spread weeds through carrying seeds on their fur/feathers, defecating the seeds at a distance from the parent plant or moving viable vegetative matter to new areas.**

Given that *G. sigillatus* is predominantly a scavenger around human dwelling, it is unlikely that it will have an important role in the spread of weeds.

e) Discuss any control/ eradication programs that could be applied in Australia if the species escaped or were released. Are any such eradication programs already available in Australia?

G. sigillatus can be easily controlled when entering human dwellings using commercial cockroach baits or surface spray insecticides. A similar strategy applied on a wider scale could be used to control or eradicate *G. sigillatus* if this species escaped or were released.

f) Behaviours that cause environmental degradation

- **Behavioural characteristics. Describe any behaviours of the species which cause physical disturbance to the environment e.g. hooves, digging etc.**

G. sigillatus does *not* possess any behavioural characteristics that are likely to cause physical disturbance to the environment. It predominantly feeds, seeks shelter and reproduces in human habitats and therefore has little opportunity to cause physical disturbance to the environment.

- **Does the species eat or disturb wetlands/wetland vegetation? This question seeks to identify negative impacts the species may have on wetlands.**

G. sigillatus does not eat or disturb wetlands/wetland vegetation. It predominantly feeds, seeks shelter and reproduces in human habitats and therefore has little opportunity to cause physical disturbance to the environment.

- **Could the species cause pollution of water bodies? This question seeks to identify if the species could impact native aquatic flora or fauna by polluting waterways.**

G. sigillatus does not reside in or around natural water bodies and therefore has little opportunity to pollute waterways.

- **If possible, outline the current health of the possible habitat matches in Australia and analyse their sensitivity to possible introductions from the species being assessed.**

The only possible habitat match for *G. sigillatus* in Australia is urbanized areas. It has only ever been recorded around human dwellings (e.g. houses, buildings) in Australia, as well as other countries where feral populations have become established (e.g. USA, Brazil). The sensitivity of the urban environment to possible *G. sigillatus* introductions is likely to be negligible as they already exist in this environment and cause little disturbance. If they enter dwelling they are easily controlled with commercial cockroach traps or surface insecticide sprays.

g) Impacts on primary industries

- **Has the species ever been recorded causing damage to: livestock, poultry, agriculture?**

G. sigillatus has *never* been recorded causing damage to livestock, poultry or agriculture.

- **Could a wild population of the species eat or damage any of the following: plant parts or products; flowers or buds; nuts; root vegetables; leaf vegetables; sugarcane; fodder crops; cotton; nursery/garden plants; timber forests or plantation trees; fruit orchards; stored grain or seeds; legumes; cereal grain in field; oilseeds or coarse grains in field; other (specify).**

G. sigillatus has never been recorded causing damage to any of the above horticultural or agricultural plants. Given *G. sigillatus* has an urban existence, the likelihood of this occurring is low.

- **Could wild populations of the species use any resources that might cause it to compete with livestock? This question seeks to identify if this species could compete with livestock.**

It is highly unlikely that *G. sigillatus* would use resources that compete with livestock. *G. sigillatus* occurs almost exclusively in human habitats and therefore there would be little overlap with livestock.

- **Has the species ever inflicted damage to trees, shrubs or their seedlings that has caused tree death or affected their value as timber? This question aims to identify if the species may have a negative impact on tree plantations/silvicultural activities.**

G. sigillatus has never been recorded to cause damage to trees, shrubs or seedlings that lead to tree death or reduces the values of their timber. This species is therefore unlikely to have a negative impact on tree plantations or silvicultural activities in Australia.

h) Damage to property

- **Could the species deface or physically damage buildings? Identify if the species could damage buildings either through physical damage, or through depositing excrement on the exterior of the building.**

G. sigillatus does not cause physical damage to buildings. It simply resides in the crevices between brickwork and pavement blocks. It does not modify these crevices in any way.

- **Could the species damage fences? Identify if the species has the capacity to damage fences.**

G. sigillatus does not have the capacity to damage fences.

- **Could the species damage equipment? Identify if the species could cause damage to domestic or commercial equipment.**

It is highly unlikely that *G. sigillatus* could cause damage to domestic or commercial equipment. Although *G. sigillatus* fills a broadly similar niche to the introduced German cockroach (*Blatella germanica*) in Australia, it does not typically enter houses or buildings. Furthermore, *G. sigillatus* does not enter equipment causing damage by chewing electrical wires. Unlike *B. germanica*, the mouthparts of *G. sigillatus* are not strong enough to chew electric cables in domestic or commercial equipment.

i) Is the species a social nuisance or danger? For example because of the following behaviours: invading buildings; forming large noisy colonies or flocks; polluting

equipment, buildings, parks or other public facilities with urine, droppings or nesting material; posing a risk to aircraft when present in flightways or at airports; other (please specify).

There is the potential for *G. sigillatus* to become a social nuisance but *not* a danger. On rare occasions, *G. sigillatus* will enter human dwellings and hide under appliances or furniture. Males calling from these positions can cause a nuisance to humans. However, *G. sigillatus* is easy to control or eradicate in these circumstances using commercial cockroach baits or surface insecticide sprays.

j) Describe any potentially harmful characteristics of the species.

- **Any potential threat to humans, any available mitigation measures (such as anti-venom), and methods for appropriate handling.**

G. sigillatus does *not* pose any potential threats to humans.

- **Has the species ever injured people? Identify whether there are any recorded instances of this species causing harm to people.**

There have not been any recorded incidences of *G. sigillatus* causing harm to people.

- **Is the species susceptible to, or could it transmit any pests or diseases? Identify if the species could potentially transmit harmful diseases or parasites to humans or any other species.**

Like most field crickets, *G. sigillatus* is susceptible to Cricket Paralysis Virus (CrPV) that already exists in native field crickets in Australia. *G. sigillatus* is also susceptible to the recently identified *Acheta domesticus* densovirus (AdDNV) that has devastated the cricket pet food industry in the United States of America (Weissman *et al.* 2012). However, AdDNV infects but does not kill *G. sigillatus*. Given the general lack of niche overlap of *G. sigillatus* and native Australian field crickets, it is unlikely that these diseases would be successfully transmitted. Most importantly, the stocks of *G. sigillatus* I wish to import to Australia have been captive bred for the last 24 generations (~3 years) and are free from the above diseases.

9. What conditions or restrictions could be applied to the import of the species to reduce any potential negative environmental impacts?

Conditions may be suggested that would reduce the impacts on the Australian environment of importing the specimen (e.g. single sex imports, desexing an animal prior to import, limiting imports to eligible non-commercial purposes only, excluding household pets etc.). If the outcome of the assessment is that the specimen can be imported subjected to conditions, it will be placed on Part 2 of the Live Import List (i.e. the regulated part of the list).

Recommended conditions should be relevant to the conservation status of the species and/or the risks posed by the import. Conditions should mitigate the likely establishment and impact that a species may have.

There are a number of conditions that can be applied to mitigate any negative impact that *G. sigillatus* may have in Australia through this import:

(i) **Limiting the import of *G. sigillatus* to non-commercial purposes *only*.** One of the major reasons for the spread of *G. sigillatus* in the United States of America (particularly southern Florida) has been the live pet food trade (Weissman *et al*. 2012). With the outbreak of the *Acheta domesticus* densovirus (AdDNV), *G. sigillatus* has been illegally imported to fill the devastating loss of *A. domesticus* stocks used predominantly to feed reptiles and predatory invertebrates (e.g. spiders). This has led to a clear increase in the number of feral populations established in this region and is also likely to explain feral populations in other countries (i.e. Australia, Brazil). The likely reason is that both consumers and producers of *G. sigillatus* are less strict with their containment of this species.

(ii) **Limiting the import of *G. sigillatus* to a secure facility.** One way to reduce the potential for *G. sigillatus* to escape and generate feral populations is to import them to a secure facility. I have a run a secure facility at the University of Exeter for the last 10 years so have vast experience of the specifications needed. This includes sealed doorways and airways and maintaining a strict cleaning protocol to ensure that any crickets escaping are contained within the secure facility and that there is no food or water available to sustain these individuals (and they will subsequently die within 48 hours). Commercial cockroach baits fitted with sticky traps should also be used to eradicate any escaped crickets in the facility.

(iii) **Limiting the import of *G. sigillatus* from specified research laboratories.** To ensure that only healthy crickets are imported and to regulate the number of imports, *G. sigillatus* should only be imported from specified research laboratories. Research laboratories, such as the one I have run for the last 10 years at the University of Exeter, maintain strict standards to ensure the health of animals and this means that excessive numbers of individuals are not required to be imported. Not all research laboratories apply the same strict standards, so limiting import from specified research laboratories will ensure these high standards are met.

(iv) **Carefully manage the breeding of imported *G. sigillatus*.** Compared to other field crickets (including native Australian species), *G. sigillatus* is highly fecund and has a much higher egg-to-adult survival. Consequently, any research program using this species will produce an excess of individuals. To efficiently and humanely regulate cricket numbers all excess crickets should be frozen overnight in a -20°C freezer that is designated for this purpose. Furthermore, crickets should be sealed in a double bag (i.e. one bag inside another) before freezing to prevent escape in the freezer and the dead crickets should be disposed of in a designated “biological waste” bin where the contents are incinerated. I

have used this protocol for the last 10 years at the University of Exeter and have not experienced any issues with escapee crickets starting feral populations in the building (this is common at other institutions using *G. sigillatus* for their research).

(v) **Import the eggs of *G. sigillatus* rather than live crickets.** With the import of any live animal, there is the risk of escape. This is particularly true with the importation of live insects where a large number of individuals are typically required. The risk of escape is greatly reduced in eggs are imported rather than live insects. Gravid female *G. sigillatus* readily oviposit eggs into moist cotton wool and these can be express couriered in sealed containers to other countries. I have done this many times between the USA and UK and have also exported the native Australian field cricket *Teleogryllus commodus* from Australia to the UK. As it takes approximately 10-12 days for eggs to hatch, this provides ample time for eggs to arrive from the UK to Australia before nymphs start hatching. Eggs are also more robust to the fluctuations in temperature experienced during transit than live crickets meaning that mortality is reduced and the use of cotton wool (as opposed to soil or peat moss) means that the risk of importing any undesirable viruses or pathogens is greatly reduced.

10. Summary of proposed activity

What is the proposed purpose of the import? Specify the reason you want to import the species. This may be for eligible non-commercial purposes such as research, education, exhibition, conservation breeding, household pet or travelling exhibition, or for commercial purposes. Where appropriate discuss:

- **The rationale for choosing to import this species into Australia.**

I have recently accepted a Professorship at Western Sydney University (Hawksbury Campus) after spending the last 10 years working in the UK (University of Exeter, Cornwall Campus). My research in the UK as a Royal Society Fellow has been examining the link between nutrition, reproduction and the evolution of lifespan. I have been using the decorated cricket, *Gryllodes sigillatus*, as a model for this research. For decades the established dogma has been that a reduction in the intake of calories extends lifespan by supressing reproduction. My research has shown, however, that this view is incorrect and that it is the balanced intake of specific macronutrients (especially protein and carbohydrates) that is responsible for this extension in lifespan. *G. sigillatus* has been an excellent model for testing this question because (*i*) this species can be easily bred in large numbers in modest space requirements due to the fact that territoriality is low in this species, (*ii*) has a relatively short development time (~6 weeks at 32°C) compared to other field cricket species (usually 2-3 months) and (*iii*) reproductive investment can be easily measured in both sexes which is difficult (if not impossible) for most species: female reproductive investment can be determined by counting the number of eggs produced, whereas male reproductive effort can be measured using electronic acoustic equipment that measures how much time a males spends calling to attract a mate.

As part of this research, I have established replicated populations of *G. sigillatus* that are evolving on different artificial diets. In each replicate, there are 5 different diets: High nutrition-Protein biased (HP), High nutrition-Carbohydrate biased (HC), Low nutrition-Protein biased (LP), Low nutrition-Carbohydrate biased (LC) and a control diet (CON, standard diet fed to cricket cultures). I have a total of 4 replicates on each of these diets, making 20 populations in total.

These populations have been evolving on these diets for the last 3 years (~24 generations) and are ready to start gathering data on the evolution of lifespan and reproduction in males and females. One of the central aims of this experiment was also to examine the effect of a rapid change in dietary conditions on the evolution of healthy aging. To do this, I was planning to switch crickets to different diets (than they evolved on) and measure the change in lifespan and a variety of health measurements (i.e. diabetes, obesity, reduction in reproductive performance). Ultimately this experiment is simulating the rapid change in dietary conditions that have occurred in humans during our evolutionary history and whether this could explain the rapid increase in health issues that have arisen in most developing countries.

- **Clearly state the numbers of animals you want to import.**

My ongoing experiment has 20 populations of *G. sigillatus* evolving on different diets. I want to import a total of 1000 eggs from each population: a total of **20,000 eggs**.

- **Discuss the interaction between males of this species. Do they need to be segregated?**

There is a low degree of territoriality between males in *G. sigillatus* which is one of the major reasons I have been able to maintain such a large set of evolving populations (discussed in section 9). The sexes in my evolving populations *must* be mixed to allow reproduction and the inevitable effects this has on lifespan.

- **If the purpose is for breeding discuss the management and control of excess progeny in the breeding program. How many animals will be kept at any time on the premises? How will lack of genetic variation be managed in the breeding program?**

Maintaining the populations on different diets and conducting the experiments I describe above will require breeding *G. sigillatus*. As I outline above (section 9), excess progeny will be managed and controlled using a strict protocol: excess crickets each generation will be sealed in a double bag, frozen at -20°C and disposed of as biological waste and incinerated. At any one time, there will be approximately 10,000 crickets at various developmental stages kept in the secure facility at Western Sydney University (please note that this is a maximum number once all populations are fully established).

Levels of genetic variation in these populations will be managed in two main ways. First, we will import more eggs (1,000 per population) than the number of adults needed (500 per

population) to ensure that a good genetic representation of crickets from my UK populations are imported. Importing fewer than 1,000 eggs per population would undoubtedly reduce the genetic variance in these populations. However, given that my populations were established from a large laboratory colony (>20,000 crickets) with ample genetic variation, importing 1,000 eggs per population should provide sufficient genetic variation. Second, as part of my regime for maintaining populations, random mating within populations is enforced to ensure genetic variation is maintained. Again, the large, genetically variable starting colony and the proposed number being imported will aid this process.

- **Discuss any other potential uses for this species should it be imported into Australia. Where applicable, describe its human uses (e.g. zoos, research, pets etc.).**

By far the biggest use for *G. sigillatus* is in the live pet food industry. As I outline above in section 9, the import of *G. sigillatus* for this purpose should be restricted to avoid potential negative implications. *G. sigillatus* is also used for research purposes, although researchers in Australia are already able to collect this species freely from established feral populations. There is the potential that other evolutionary biologists will use the *G. sigillatus* populations I hope to import in their research program via collaboration. If this is the case, they will need to seek the relevant State permits and have the appropriate secure facilities to do so, if wanting to work with live crickets. Alternatively, they may opt to process non-living *G. sigillatus* samples which I will make readily available to them after seeking any relevant permits.

- **Provide details on where animals are obtained, e.g. captive bred populations or from the wild.**

The *G. sigillatus* being imported were originally collected (a total of 500 mated females) from New Mexico (United States of America) in 2009. However, this starting colony was maintained in the laboratory for 32 generations (~4 years) prior to establishing my diet populations and have been maintained for a further 24 generations (~3 years) in my experiment. In total, the crickets have therefore spent 56 generation (7 years) in captivity.

11. Guidelines on how species should be kept

As appropriate discuss the following issues:

- **What are the standards for transporting animals? Will the animals be transported according to International Air Transport Association (IATA) regulations?**

The IATA regulations have largely been established for the transport of larger, vertebrate species that require a much higher standard to ensure the health and wellbeing of transported animals. To the best of my knowledge, there are no such standard available for insects and most are transported by couriers with the relevant import licences. I plan to

transport the eggs of *G. sigillatus* (oviposited into moist cotton wool) in sealed containers to Australia using the courier DHL (www.dhl.co.uk) which readily transports such material. Eggs take 10-12 days to hatch in *G. sigillatus* and can be couriered from the UK to Australia in 5-6 days, ensuring that eggs do not hatch en route. I have used this courier many times previously to transport cricket eggs from Australia to the UK and have never experienced any difficulities.

- **How does enclosure size relate to territory requirements?**

Each of my experimental populations will be maintained in a single plastic container measuring 50 x 50 x 25 cm (length x width x depth) that contains an abundance of cardboard egg carton for shelter (which greatly increases the internal area of the container), water and artificial diet. The low territoriality of this species, as well as the abundance of resources (which reduces competition and territoriality), will ensure that the container size is appropriate for the degree of territoriality in *G. sigillatus*.

- **Discuss the containment and management standards for Australia e.g. the proportion of males to females and the maximum number that should be kept in enclosures/aquaria. Also if single sex populations would be contained within enclosures to limit breeding etc**.

As outlined above, each experimental population will be maintained in a single plastic container measuring 50 x 50 x 25 cm (length x width x depth) that contains an abundance of cardboard egg carton for shelter, water and artificial diet. Each population will contain approximately 500 crickets in a 50-50% sex ratio that is required for successful breeding (and maintaining genetic variation in populations). Given the low territoriality of *G. sigillatus* and the abundance of resources, this level of containment and management is more than appropriate. It is important to note that these same conditions are used to maintain my populations in the UK (and have been for 24 generations) and I have not experienced any issue with the health or wellbeing of crickets.

- **What standards are used for the enclosures/aquaria in which this species would be kept? What are the best practice standards? Who applies these standards? Will enclosures/aquaria be sufficiently large enough for the humane containment of the animals? For example providing sufficient depth and length?**

There are no formal standards for keeping *G. sigillatus*. The choice of container size and best practise standards I apply is self-imposed and based on 10 years of working with this particular cricket species and over 20 years working with insects. As these crickets are to be used for research purposes, specifically examining the effect of diet on health and lifespan, it is central that they are both humanely contained and in good health. The containers and best practise standards I outline above are the same I have been using in the UK to maintain these populations for the last 3 years and I have never experienced any problems with

cricket health. This demonstrates that the size of the container, as well as the abundance of food, water and shelter, is optimal for the healthy containment of these crickets.

- **Address welfare issues in housing captive specimens.**

Each *G. sigillatus* population is provided with an abundance of shelter (cardboard egg carton), food and water. Food and water are checked daily and replaced as needed to ensure they always have an *ad libitum* supply. Each population is cleaned weekly to remove faeces or any dead individuals and containers are sterilized (using bleach) between generations. Both practises help prevent the spread of disease. As the sole purpose of importing these *G. sigillatus* populations is for research examining the effect of diet on lifespan and health, it is paramount to maintain a high welfare standard. All the procedures I have outlined above for the maintenance and rearing of these *G. sigillatus* populations are currently in use in the UK and represent best practise. In the 3 years of maintaining these experimental populations, I have not had any issue with welfare or cricket health.

12. State/Territory controls

Outline any Commonwealth, state, or territory legislative controls on the species and provide information on any other relevant assessments that have been made of the species.

As each state and territory of Australia has different legislation regarding legally keeping different species, and some states/territories prohibit keeping certain animals, therefore please check what the restrictions each state/territory imposes.

Are you aware of quarantine requirements for bringing live animals into Australia? Is the species you are proposing to have added to the Live Import List allowed to be imported under the *Quarantine Act 1908*? Does an import permit need to be obtained from AQIS?

If not, contact Biosecurity Australia to discuss the undertaking of an Import Risk Analysis (IRA) by telephone on (02) 6272 3933 or visit their website for more information at www.BiosecurityAustralia.gov.au.

There are no known controls at this time.

Reference list

Archer CR, Zajitschek F, Sakaluk SK, Royle NJ & Hunt J. (2012) Sexual selection affects the evolution of lifespan and ageing in the decorated cricket *Gryllodes sigillatus*. *Evolution* 66: 3088-3100.

Bailey, WJ & Haythornthwaite S (1998) Risks of calling by the field cricket *Teleogryllus oceanicus*: potential predation by Australian long-eared bats. *Journal of Zoology* 244: 505-513.

Burpee DM & Sakaluk SK (1993) Repeated matings offset costs of reproduction in female crickets. *Evolutionary Ecology* 7: 240-250.

Chintauan-Marquier IC, Legendre F, Hugel S, Robillard T, Grandcolas P, Nel A, Zuccon D & Desutter-Grandcolas L (2016) Laying the foundations of evolutionary and systematic studies in crickets (Insecta, Orthoptera): a multilocus phylogenetic analysis. *Cladistics* 32: 54-81.

Luong LT & Kaya HK (2005) Sexually transmitted nematodes affect spermatophylax production in the cricket, *Gryllodes sigillatus*. *Behavioural Ecology* 16: 794-799.

Otte D & Alexander RD (1983) *The Australian Crickets (Orthoptera: Gryllidae)*. Monograph 22, Academy of Philadelphia, Allen Press, Kansas. Pages 160 – 162, Illustrations (page 161, Figures 119 and 120).

Otte D (2006) *Gryllodes sigillatus* (Walker) is a valid species distinct from *Gryllodes supplicans* (Walker). *Transactions of the American Entomological Society*, 132: 223-227.

Rodriquez-Munoz R, Bretman A, Slate J, Walling CA & Tregenza T (2010) natural and sexual selection in a wild insect population. *Science* 328: 1269-1272.

Rodriquez-Munoz R, Bretman A & Tregenza T. (2011) Guarding males protect females from predation in a wild insect. *Current Biology* 21: 1716-1719.

Sakaluk SK (1987) Reproductive behaviour of the decorated cricket, *Gryllodes supplicans* (Orthoptera: Gryllidae): calling schedules, spatial distribution and mating. *Behaviour* 100: 202-225.

Sakaluk SK & Belwood JJ (1984) Gecko phonotaxis to cricket calling song: a case of satellite predation. *Animal Behaviour* 32: 659-662.

Wagner WE (1996) Convergent song preferences between female field crickets and acoustically orienting parasitoid flies. *Behavioural Ecology* 7: 279-285.

Walker TJ (1964) Experimental demonstration of a cat locating orthopteran prey by the prey's calling song. *Florida Entomologist* 47: 163-165.

Weissman DB, Gray DA, Pham HT & Tijssen P (2012) Billions and billions sold: pet-feeder crickets (Orthoptera: Gryllidae), commercial cricket farms, an epizootic densovirus, and government regulation make for a potential disaster. *Zootaxa* 3504: 67-88.

Zajitschek F, Brassil CE, Bonduriansky R & Brooks RC (2009) Sex effects on lifespan and senescence in the wild when dates of birth and death are unknown. *Ecology* 90: 1698-1707.