OVERWINTERING BIOLOGY OF THREE CALAPHIDINE APHIDS (HEMIPTERA: STERNORRHYNCHA: APHIDIDAE) AND OBSERVATIONS ON OTHER APHID SPECIES

Dinah F. Hales

Independent Researcher: dfhales@hotmail.com

Summary

This paper reports the overwintering biology of aphid species in Sydney NSW, including *Sarucallis kahawaluokalani* (Kirkaldy) and *Shivaphis celti* Das, both recently arrived in Australia. *S. kahawaluokalani* is shown to be holocyclic and monoecious, i.e. produces sexual forms in autumn and lays overwintering eggs on its single host, crape myrtle. No sexual individuals of *S. celti* were found by the end of observations and it is provisionally considered as anholocyclic (continuously parthenogenetic) in the Sydney region. Likewise, only one ovipara (no males) was found amongst large populations of *Tinocallis ulmiparvifoliae* Matsumura, and it appears also to be functionally anholocyclic. These three species are all members of the sub-family Calaphidinae. Observations on the diversity of other aphid species are noted and discussed in terms of recent climatic events.

Key words *Shivaphis*, *Sarucallis*, *Tinocallis*, annual cycle, holocyclic, anholocyclic, diversity, climate.

INTRODUCTION

The aphids present in Australia were reviewed by Eastop (1966) and have been added to since by various authors. Most recently, Brumley (2020) published a substantial paper on aphids present in the Australian National Insect Collection, and added new species present in the collection but either unpublished or re-identified. He also noted 24 species not in the collection but published, giving a check list of aphids found so far in Australia. Exotic aphid species continue to arrive in Australia, commonly by air travel or in freight. A recent government report on quarantine risks of imported cut flowers noted that 21 aphid species were a quarantine risk including six not yet in Australia, and further that aphids rank No. 3 on the list of arthropods intercepted at quarantine (anon., Australian Government, 2019). Aphids are often discovered by biosecurity agencies, by accident, or by obvious effects on commercial crops of agricultural, horticultural or forest products.

Aphids have varied complex annual cycles, summarised for example by Blackman and Eastop (1994). Clonal parthenogenetic viviparous reproduction may be continuous throughout the year: this is known as anholocycly and is common in many exotic aphids naturalised in Australia. It allows rapid establishment, colony growth and spread. Some aphids hatch from eggs laid on the primary host and have successive generations on plants of the same species, eventually producing males and egg-laying females (oviparae) in the autumn. This is known as monoecious holocycly and as well as providing a non-feeding overwintering stage, it allows for genetic recombination so that new clones will arise from eggs that hatch in the spring. Finally, some aphids produce males and mating females in a two-stage process and migrate from their summer (secondary) hosts to a winter (primary) host where the eggs are laid and the first spring parthenogenetic generations live. The winter host, often a deciduous tree, is taxonomically distinct from the usually herbaceous summer host (hosts). Annual cycles of this kind are known as holocyclic and heteroecious.

The crape myrtle aphid *Sarucallis kahawaluokalani* (Kirkaldy) was discovered at the commencement of the work reported in this paper. Its detection as a new biosecurity incursion to Australia is reported separately (Hales and Gillespie 2020). Colour photographs are available online, e.g. Kondo and Simbaqueba (2014). It is monoecious and holocyclic on crape myrtle, *Lagerstroemia indica* L. wherever its annual cycle has been studied.

Shivaphis celti Das is another Asian calaphidine species recently arrived in Australia. It can be either monoecious holocyclic (e.g. in USA, Halbert and Choate 2003) or anholocyclic (e.g. in Taiwan, Blackman and Eastop 2020). *Shivaphis celti* was first reported in Australia in 2013 after discovery during biosecurity surveillance (The National Plant Biosecurity Status Report 2013, published 2014; Ridgeway and Burgess-Buxton 2014, Carnegie and Nahrung 2019). It seemed worthwhile to pursue its biology on its host, *Celtis* spp. (Cannabaceae, hackberries). There are three introduced species of hackberries in NSW, *C. sinensis* Pers. (Chinese hackberry), *C. australis* L. (European hackberry) and *C. occidentalis* L. (American hackberry). All are known hosts of *S. celti* elsewhere. Of these, *C. sinensis* is the most common in NSW: it is a fast-growing, invasive, bird-distributed plant and declared noxious weed, affecting bushland, gardens and agricultural land (NSW Department of Primary Industries, 2017). Colour photographs of the aphid are available on-line, e.g. Halbert and Choate (2003), Lawson and Dreistadt (2019).

Unquantified observations in recent years suggested a decline in aphid diversity. During the COVID lockdown, a Moericke yellow trap was run in Beecroft NSW to survey diversity of aphids in the area. The trap was running through autumn and winter, and thus had the potential to give information on the annual cycles of aphids collected.

MATERIALS AND METHODS

A Moericke yellow trap was prepared by painting a 40 cm x 48 cm tray yellow (White Knight Rustguard Epoxy Enamel shade Golden Yellow) and exposing it at a height of approximately 1.5 m above the ground in positions not overhung by trees, at latitude -33.7542 and longitude 151.0595. The tray was filled with water to which a small amount of dishwashing detergent was added. Aphids were removed from the trap daily from 19 April 2020 between 16:00 and 17:00 h, placed in 80% ethanol, counted, identified as far as possible using a Zeiss stereoscopic dissecting microscope, and separated by sex (winged viviparous females, winged males). Females were identified as viviparous by observation of embryos within the body, distinguishable by their red eyes. Males were readily identified by their black claspers. Data for this paper were collected until the end of August, but yellow trapping continued.

Some specimens had to be mounted and examined with compound microscope resolution. Slides were made by the PVA-borax-glycerol technique (Blackman and Eastop 2020), with modifications by the author to replace chemicals that were difficult to obtain in Australia or without an institutional base, as below.

1. Methylated spirit instead of ethanol
2. Sodium hydroxide instead of potassium hydroxide
3. Elmer's Glue instead of clear Pritt glue, which is not available in Australia.

Specimens were divided into putative species groups after assessment of the following metrics: number of rhinaria on the 3rd and 4th antennal segments, ratio of the processus terminalis to the base of the 6th antennal segment, shape of siphunculi and cauda and the ratio of their lengths, wing venation, antennal tubercles, abdominal pigmentation. Published keys (Eastop 1966) enabled refinement of the data and were supplemented by online material to cover species that have arrived more recently.

The first trap was a paler yellow than ideal, and faded with exposure. A second, brighter yellow trap, consisting of a yellow plastic home ware tray, 48 cm x 33 cm (water surface), was set up on 19 July approximately 1 m from the first. Trees near the traps i.e., crape myrtle trees (*Lagerstroemia indica*, Lythraceae, approximately 20 m from the trap), Chinese hackberry (*Celtis sinensis,* approximately 10 m and 200 m from the trap) and Chinese elm (*Ulmus parvifolia* Jacq., Ulmaceae, approximately 300 m from the traps) were inspected for aphids during the same time as the collections from the traps. Once males of *S. kahawaluokalani* were found in the trap, five leaves per day randomly collected from crape myrtle suckers were examined and counts were made of all aphids observed i.e., males, parthenogenetic females, and wingless individuals identified as oviparae by their thickened hind tibiae, which bear sex pheromone glands. All parthenogenetic females in this species are winged. Twigs were examined for eggs.

Shivaphis celti was rarely collected in the trap, despite the nearby presence of its host plant. Populations on trees and saplings tended to be small and daily destructive sampling was not feasible. Non-destructive sampling was not feasible either, because the very long and dense coating of wax filaments on living specimens makes it difficult to identify the sex, instar or female reproductive morph (viviparous or sexual). Twigs of *C. sinensis* bearing colonies were collected every few days, and adults were determined to morph, sex and reproductive type. In this species, parthenogenetic females can be winged or wingless. The search effort was not standardised: searching continued until an adequate sample was obtained. Predators and parasites present near or among colonies were noted for all three species. Weather data for temperature and rainfall were obtained from the nearest Bureau of Meteorology weather station at North Parramatta (approximately 7.2 km to the south west of the traps and trees).

RESULTS

Sarucallis kahawaluokalani

S. kahawaluokalani was found in large numbers in the trap from the first day of collecting. Fig. 1 shows the daily numbers of *S. kahawaluokalani* winged viviparous females and males caught in the yellow trap. The first male of this species was collected in the yellow trap on 29 April and counts on 5-leaf samples over the following days demonstrated the presence of oviparae and males, but the majority of specimens were winged viviparous females (Table 1). The first eggs were observed on 6 May, near the leaf buds and in fissures in the bark (see also Lazzari and Zonta-De-Carvalho 2006) confirming the monoecious holocycly of this species in Sydney. No further viviparous females were caught in the yellow trap after 24 May. Crape myrtle plants had lost nearly all their leaves by the end of May, and leaf buds began to open in the last week of August. A few larval fundatrices were observed in late October and early November but no new colonies have yet been seen.

Table 1. Viviparous and sexual *Sarucallis kahawaluokalani* from 5-leaf samples of crape myrtle.

Date	Winged viviparae	Males	Oviparae	Eggs
30 April 2020	18	2	present nc	
1 May 2020	15	5	8	
2 May 2020	8	2	3	
3 May 2020	21	3	3	
4 May 2020	21	0	9	
5 May 2020	28	3	5*	
6 May 2020	nc	nc	1	Yes, from 3 sites

* one was observed aborting an embryo, i.e. it had intermediate reproductive characteristics. nc= not counted
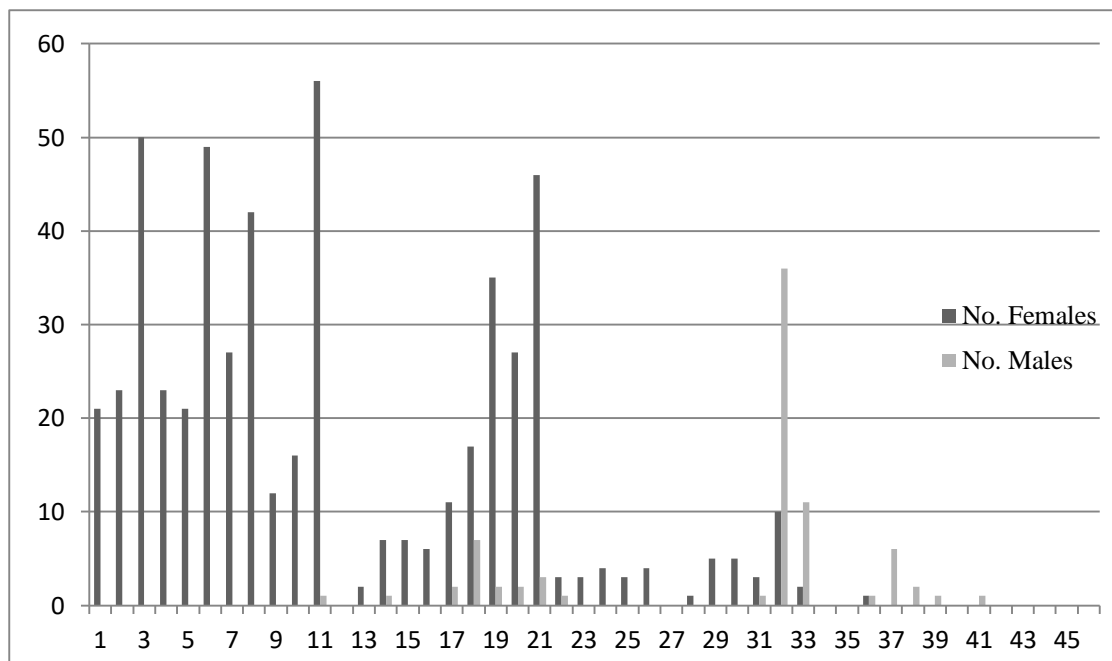

Figure 1. Daily yellow trap catches of male and female (winged viviparae) *S. kahawaluokalani*. Day 1 is 19 April 2020, Day 44 is 1 June 2020. Numbers of females and of males per day. No further viviparous females were caught after 24 May. Leaf fall of the crape myrtle host plant was almost complete by the end of May.

Catch size (Fig. 1) was smaller when the daily maximum was <20 °C (data not shown, see Bureau of Meteorology 2020). The maximum temperature for the preceding 24 h is taken at 09:00 h, so it is actually the maximum for the previous day. It was observed that most aphids were captured between 12:00 and 16:00 h, with few present in the trap before midday. At their peak, specimens of this species were found on many non-host plants and in spider webs.

Shivaphis celti

Few specimens were caught in the yellow traps (one on 9 May 2020, two on 30 May 2020, one on 13 June 2020, one on 31 July 2020). The two caught on 30 May 2020 gave a clue to the low success rate. They were observed floating on the surface with wings and body clear of the water, so that they could potentially sail to the edges and wade or climb ashore. The long wax filaments on legs and body (see colour photographs online, e.g. Halbert and Choate 2003) gave at least temporary protection from immersion. Wax filaments on aphids are often found on species living in dense colonies in confined spaces, where the wax prevents smothering of the aphids by honeydew (Smith 1999). *S. celti* does not live in dense colonies or in confined spaces, but does often live on the upper surface of leaves and is at risk from honeydew falling from above. According to Pike *et al.* (2002), wax filaments may also disguise aphids from predators.

Apart from this, *S. celti* may be less attracted to the spectral characteristics of the traps than is *S. kahawluokalani*. *S. celti* was readily identifiable in the aeroplankton as "flying fluff", and was common in the air in comparison with the trap catch. Collections from leaves and twigs of the host plant, Chinese hackberry, regularly provided winged and wingless viviparous females (Table 2) until mid-August. No males or oviparous females were detected. A proportion of females showed intermediate characteristics, having very small wings reaching approximately to the apex of the hind coxae. These were recorded as intermediates in the later collections (Table 2). The aphids had the appearance of wingless viviparae in other regards, were well developed and contained embryos.

Tinocallis ulmiparvifoliae

Winged females of *T. ulmiparvifoliae* were found in the yellow trap from the beginning of May to mid-June, the total number being 12 specimens. Leaf collections from *U. parvifolia* commenced in early June and provided very dense colonies during the first two weeks (60+ winged viviparous females per collection). The population crashed in the third week (16 specimens) and the aphids were almost gone in the fourth week (2 specimens). A single wingless ovipara was found on 13 June 2020 but no males

were collected. Evidence of intense coccinellid predation was observed, with larvae, larval exuviae and pupae observed as well as adults. The ladybird *Harmonia testudinaria* (Mulsant) was the most common predator species. By the end of June, leaf fall was advanced, but trees retained some leaves throughout winter.

Other Species Trapped

Other aphid species were collected in small numbers in the traps. Table 3 shows numbers of each species trapped, consolidated into time segments of about two weeks. They were *Hyperomyzus lactucae* (L.) (sow-thistle aphid), *Aphis (Toxoptera) citricidus* (Kirkaldy) (brown citrus aphid), *Macrosiphoniella sanborni* (Gillette) (chrysanthemum aphid), *Myzus hemerocallis* Takahashi (day lily aphid), *Macrosiphum euphorbiae* (Thomas) (potato aphid, polyphagous), *Aphis spiraecola* Patch (polyphagous), *A. gossypii* Glover (polyphagous), *Brachycaudus*, unidentified species, *Rhopalosiphum padi* (L.) (grasses and cereals), *Aulacorthum solani* (Kaltenbach) (polyphagous), *Megoura crassicauda* Mordvilko (broad beans, vetches), *Takecallis arundinariae* (Essig) (bamboo), *Dysaphis tulipae* (Boyer de Fonscolombe), (polyphagous on monocots) and *Tetraneura fusiformis* Matsumura (grass root aphid). *Tetraneura* is generally anholocyclic in Australia but elsewhere alternates between grasses and elms where aphids hatching from eggs form galls on the spring leaves. Two winged male aphids were collected on 1 August 2020 and 5 August 2020. They could not be identified but resembled *Rhopalosiphum*.

Species observed on host plants

Casual observations on garden or street plants yielded species as follows, to give a total of 22 putative species.

1. *Aphis gossypii* Glover, on cobbler's pegs, *Bidens pilosa*. This host plant was not given in the account by Brumley (2020), i.e. it is not recorded in the ANIC holdings. Anholocyclic. Also in yellow trap.
2. *Aphis (Toxoptera) aurantii* Boyer de Fonscolombe, black citrus aphid, on a range of plants including *Camellia*, *Gordonia*, *Cordyline* spp., *Celtis*. These host plants were not given in the account by Brumley (2020). Anholocyclic.
3. *Pseudoregma panicola* (Takahashi) on seed heads of the grass *Oplismenus* sp. Possibly holocyclic and heteroecious with *Styrax* as primary host but probably anholocyclic in Australia.
4. *Schoutedenia ralumensis* Rübsaamen on the native shrub *Breynia oblongifolia*. Holocyclic and monoecious, with sexual forms produced through the summer.

Table 2. Collections of *Shivaphis celti* from Chinese hackberry, May-August 2020.

Date	Winged viviparae	Wingless viviparae	Date	Winged viviparae	Wingless viviparae
6 May	1	1	11 June	2	23
10 May	11	9	19 June	13	11
11 May	4	10	26 June	1	6 (3 intermediate)
15 May	4	10	3 July	2	5 (2 intermediate)
19 May	3	15	10 July	0	14 (4 intermediate)
24 May	4	5	18 July	8	2
28 May	0	6	24 July	1	0
2 June	2	4	31 July	1	0
5 June	1	15	7 August*	1	0

* no further specimens observed during August.

Table 3. Viviparous female aphids trapped through April-August 2020 at Beecroft NSW.

Species/Dates*	A	B	C	D	E	F	G	H	I
Sarucallis kahawaluokalani	340	175	27	0	0	0	0	0	0
Hyperomyzus lactucae	3	0	1	0	0	0	0	0	0
Aphis spiraecola	4	2	1	0	3	0	3	5	9
Rhopalosiphum padi	1	0	0	0	0	0	0	3	0
Aphis citricidus	1	0	0	0	0	0	0	0	0
Macrosiphum euphorbiae	1	0	0	0	0	0	0	0	0
Dysaphis tulipae	1	0	0	0	0	0	0	0	0
Tinocallis ulmiparvifoliae	0	4	5	3	0	0	0	0	0
Myzus hemerocallis	0	1	0	0	0	0	0	0	0
Macrosiphoniella sanborni	0	1	0	0	0	0	0	0	0
Shivaphis celti	0	1	2	1	0	1	0	0	0
Aphis gossypii	0	1	1	0	0	0	0	0	0
Tetraneura fusiformis	0	0	0	1	1	0	1	0	0
Takecallis arundinariae	0	0	0	0	0	1	0	0	0
Brachycaudus sp.#	0	0	0	0	0	0	2	0	0
Megoura crassicauda	0	0	0	0	0	0	0	0	1
Aulacorthum solani	0	0	0	0	0	0	0	0	1

* Notes. Date ranges: A:19-30 April; B: 1-15 May; C: 16-31 May; D: 1-15 June; E: 16-30 June; F: 1-15 July; G: 16-31 July; H: 1-15 August; I: 16-31 August.
\# The *Brachycaudus* specimen keyed to the genus *Brachycaudus* but did not fit the characteristics of any of the species known from Australia. It was also unusual in having the two branches of the media of the forewing originating very close together. The data for *Sarucallis kahawaluokalani* are further dissected in Figure 1.

5. *Macrosiphum rosae* (L.), rose aphid. Mainly anholocyclic in Australia but retains some ability to produce sexual forms in experimental conditions (Wöhrmann *et al.* 1991).

6. *Periphyllus californiensis* (Shinji). Immatures observed at the end of August on Japanese maple. Holocyclic, monoecious and with aestivating dimorphs (see Eastop 1966).

A notable absentee from trap and field observations was the oak aphid *Tuberculatus annulatus* (Hartig), usually present in nuisance proportions through its production of honeydew which drops and encourages the growth of black fungi on vehicles. The aphid re-appeared in spring and was first observed on oak leaves on 4 October 2020, concurrent with the second flush of leaves. Table 4 lists the aphids trapped in 1961 from April to August at Rydalmere NSW (Hughes *et al.* 1964), and the aphids trapped or observed in the present study for the same period in 2020.

Predators and Parasites
Coccinellids including *Coelophora inaequalis* (F.), *Coccinella transversalis* F., *Harmonia conformis* (Boisduval), *H. testudinaria*, *Halmus chalybeus* (Boisduval) and *Apolinus lividigaster* (Mulsant) were found in association with colonies of *S. kahawaluokalani*, *S. celti* and *T. ulmiparvifoliae.* Neuropteran and syrphid larvae were also found. Occasional parasitisation by aphidiid wasps was noted for *T. ulmiparvifoliae.*

By-catch
The trap by-catch during autumn consisted mainly of Diptera, ranging from minute to blowfly size. Occasional moths, psyllids, psocopterans, and hymenopterans, including on one day a swarm of flying ants, made up most of the rest of the catch. A single minute weevil was trapped, as were occasional spiderlings.

DISCUSSION
Eastop (1966) summarised the change in annual cycles of holocyclic holarctic aphids transported to milder environments such as those in many parts of Australia: the holocycle is frequently lost or sometimes disrupted so that sexual forms are produced in spring. This could suggest aestivating eggs, as in native aphids of the genus *Neophyllaphis*. These aphids have a short active period on their host (*Podocarpus* spp.) in late winter-early spring, and then sexual production followed by aestivation-hibernation until the following year (Hales 1976). Aestivating eggs have not been confirmed in non-native aphids. At least some non-native species retain the holocycle, particularly those monoecious on deciduous trees.

Sarucallis kahawaluokalani
First described by Kirkaldy in 1907 from Hawaii, this species has been extending its range from its east-Asian origins. Hales and Gillespie (2020) give information on its spread. It is known as holocyclic and monoecious wherever its annual cycle has been studied, and it is unsurprising to find the same situation in the Sydney area. Whilst many introduced aphids in Australian conditions have lost the ability to produce sexual forms, this is less likely in a newly arrived species, especially one specific to a deciduous tree such as *Lagerstroemia*. The occasional host *Lawsonia* occurs naturally in northern Australia and is said to be drought-deciduous. Small numbers of fundatrices (the morph that hatches from the eggs) suggest that winter conditions were unfavourable for egg survival, perhaps being too dry. It is too early to predict likely future population sizes in either NSW or other states.

Shivaphis celti
Like *S. kahawaluokalani*, *S. celti* is a recently-arrived species in Australia. It is specific to a semi-deciduous host-plant, with younger trees retaining leaves through to mid-August, and fresh shoots being continuously produced on saplings and in response to damage by possums. New leaves commenced growing from mid-August on mature trees, so potential food sources were constantly available. The species appears to be anholocyclic, with no sexual forms observed during April-August inclusive. It is known to be holocyclic elsewhere, though in Taiwan it is mainly anholocyclic with some sexual individuals observed in December and January, equivalent to June-July in the southern hemisphere. The short-winged individuals were common enough that they could be considered a separate morph rather than an occasional error in development. I have used the term "intermediate" in this paper rather than vestigial-winged or brachypterous. Brachypterous morphs are known in other aphids, for example *Drepanosiphum dixoni* (Dixon 1972). The aphid is expected to survive well in other states provided *Celtis* spp. are present.

Ridgeway and Burgess-Buxton (2014) stated that the aphid was first recorded in Australia in September 2013 on blackberry plants from China, and subsequently found in Mascot NSW and Camperdown NSW. Their observations in March 2014 of large populations on hackberry along the Hawkesbury and Parramatta Rivers indicate that it was probably here earlier. The aphid caused defoliation of saplings and partial defoliation of mature trees during summer 2014 in those areas. In contrast, in the present study populations were small on most trees and were unlikely to have caused damage. Nevertheless, young saplings died or were defoliated and there was leaf loss from mature trees during summer: this seemed to be a result of drought

Table 4. Comparison of aphid species caught at Rydalmere, April-August 1961, and aphid species caught/observed in Beecroft, April-August 2020.

Hughes (1961) April-August inclusive	Hales (2020) April-August inclusive
Aphis craccivora	
*Aphis gossypii**	*Aphis gossypii*
*Aphis nerii**	
	Aphis spiraecola
	Aphis (Toxoptera) aurantii#
Toxoptera citricidus	*Aphis (Toxoptera) citricidus*
*Hyalopterus pruni***	
*Melanaphis bambusae***	
*Rhopalosiphum maidis**	
Rhopalosiphum padi	*Rhopalosiphum padi*
*Rhopalosiphum rufiabdominale**	
Schizaphis graminum	
*Aulacorthum solani***	*Aulacorthum solani*
Brachycaudus helichrysi	*Brachycaudus* sp.
Brevicoryne brassicae	
Capitophorus elaeagni	
*Capitophorus hippophaes javanicus***	
*Cavariella aegopodii**	
*Chaetosiphon tetrarhodum***	
Dysaphis foeniculus	
*Dysaphis tulipae***	*Dysaphis tulipae*
*Hyadaphis foeniculi***	
*Hyperomyzus lactucae**	*Hyperomyzus lactucae*
Lipaphis pseudobrassicae (as *erysimi*)*	
*Macrosiphoniella sanborni***	*Macrosiphoniella sanborni*
*Macrosiphum euphorbiae**	*Macrosiphum euphorbiae*
*Macrosiphum rosae***	*Macrosiphum rosae#*
*"Macrosiphum avenae"***	
*Myzus cerasi***	
	Myzus (Myzus) hemerocallis##
*Myzus ornatus***	
*Myzus persicae**	
*Neotoxoptera oliveri***	
*Ovatus crataegarius***	
*Rhodobium porosum***	
*Myzocallis castanicola***	
Tuberculatus (as *Myzocallis*) *annulatus***	
	Shivaphis celti##
*Tinocallis ulmiparvifoliae***	*Tinocallis ulmiparvifoliae*
Tetraneura (as *hirsuta*)*	*Tetraneura fusiformis*
	Sarucallis kahawaluokalani##
	Schoutedenia ralumensis#
	Pseudoregma panicola#
	Takecallis arundinariae##
	Megoura crassicauda##
	Periphyllus californiensis#
36 species	22 species
* >50 trapped April-August ** < 5 trapped April-August	# observed in field, not trapped ## new to Australia since 1961

Notes. Some aphids that were common in the 1961 collection were absent from the 2020 collection, viz. *Aphis nerii*, *Rhopalosiphum rufiabdominale*, *Cavariella aegopodii*, *Lipaphis pseudobrassicae*, *Myzus persicae*. All these species are easy to identify unambiguously and their host plants are common in the area.

and high temperatures in 2020 rather than aphid damage. There is also a native *Celtis*, *C. paniculata* (Endl.) Planch. Ridgeway and Burgess-Buxton (2014) suggested that it could be adversely affected by this aphid. The species is present in Ipswich, south-east Queensland (White, pers. comm.).

Tinocallis ulmiparvifoliae
T. ulmiparvifoliae has been in Australia since at least 1933 (Zeck 1933, cited by Blackman and Eastop 2020) and may have been introduced on multiple occasions since, for example with import of bonsai trees. It was present in large numbers on small-leafed elms until early June, but without producing males. Neither Eastop (1966) nor Blackman and Eastop (2020) comment on its annual cycle in Australia, though the latter source mentions sexual individuals in some Asian countries, and other *Tinocallis* species are known to be holocyclic. The finding of a single oviparous female suggests loss of the full holocycle in the population studied and it would be interesting to know how widely this situation occurs in Australia. The study trees retained some leaves through winter.

Comparison with prior trapping studies
Hughes *et al*. (1964, 1965) coordinated yellow trapping over a transect from Far North Queensland to Tasmania during the years 1961 and 1962. They discussed the characteristics and limitations of yellow traps. Their trapping location at Rydalmere NSW was approximately 6.7 km to the south-west of the yellow traps in this study and can be used for comparison with the present findings. The Rydalmere traps collected 45 species in 1961 and 46 in 1962, with the highest numbers of species and individuals in April and May (23 and 24 species, 1961) and 36 different species from April-August inclusive. In the present study, 22 species were collected or observed in the same months (April only from 19th). There is an overlap of twelve species with the 1961 Rydalmere list for the April - August period. This low figure results from loss of species common in 1961, and addition of species that have arrived since 1961, but mainly in the last 15 years. The number of aphidid species recorded in Australia has increased by about 57 species from 114 species in the early 1960s (Eastop 1966), to over 170 recorded by Brumley (2020), including newly-described native species and newly-arrived exotic ones. Thus, the number of species has increased by 50%. Potentially the diversity at a given site might increase by the same factor, but this was not observed. The striking features of the current data are, firstly, the absence in 2020 of species caught in large numbers in 1961 (marked * in Table 4) and secondly, the addition of species not known in Australia at the time of the 1961 collections (marked ##).

Hughes *et al*. (1964, 1965) concluded that the numbers and species of aphids in a trap reflected the sorts of plants in the area. The trap in the current study was in suburban Sydney, about 200 m from bushland, and surrounded by a diversity of ornamental plants, garden flowers, vegetable gardens, weeds, grasses and fruit trees. These could potentially serve as host plants for more aphid species than found.

Successive checklist numbers are accumulations of all species recorded from Australia, and do not provide information on extinction or changes in population size or distribution. Single records from the past may reflect transient establishment of species. Environmental parameters (e.g. temperature, host plant condition or availability especially in the case of holocyclic species) may constrain populations, but these factors are unlikely to explain the loss of *Aphis nerii* Boyer de Fonscolombe (oleander aphid), *Rhopalosiphum rufiabdominale* (Sasaki) (rice root aphid), *Cavariella aegopodii* (Scopoli) (carrot and parsley aphid), *Lipaphis pseudobrassicae* (Davis) (turnip aphid) and *Myzus persicae* (Sulzer*)* (peach-potato aphid, polyphagous). Could their disappearance be due to climate change? Are they now more common in cooler climates? Local surveys in other regions could clarify their distribution.

Annual cycle: environmental triggers and physiological response
In considering evolution of the annual cycles of *Sarucallis*, *Shivaphis* and and *Tinocallis* in Australia, we need to consider the abiotic factors that control production of sexual forms. This may suggest future evolution of the cycles, and may also throw light on changes in distribution of other species.

The main abiotic factors are temperature and photoperiod, or more accurately the length of the dark period (scotoperiod). This is a two-stage epigenetic process, with males being produced in response to a characteristic scotoperiod for the particular clone, provided the temperature is low enough. The physiological response is mediated by light receptors in the mother's brain, initiating a hormonal cascade that results in loss of an X-chromosome during the parthenogenetic formation of the oocyte. The resultant embryo will therefore develop as a male with X0 sex chromosome complement. At around the same time, and again in response to scotoperiod and temperature, some parthenogenetic winged females of heteroecious species depart for the primary (winter) host, where they give birth to female offspring (oviparae) usually destined to be wingless. They produce eggs after mating with the males. These females are determined as oviparae later in embryonic

development than the males, and are ready to mate when the males arrive at the primary host. The result is that the aphids complete oviposition before leaf fall has made the trees unsuitable for continued parthenogenetic reproduction. The stimuli to the aphids to produce sexual forms are the same as those that promote leaf fall, so the two procedures are closely coordinated. Host plant condition may also influence the induction of sexual forms but is not usually an essential trigger. In non-alternating aphids, the egg-producing females can be born to either winged or wingless parthenogenetic mothers.

The level of juvenile hormone is said to have a controlling role in determination of sexual forms (Ishikawa *et al*. 2012), and there has been much recent research at the gene level, but the series of physiological events between the environmental stimuli and the control of gene activity is still unclear. The temperature and scotoperiod thresholds vary among clones, among species and with latitude. For a review of factors inducing sexual reproduction see Le Trionnaire *et al*. (2008). Hales *et al*. (1997) discussed annual cycles in relation to population genetics.

Climate change and anthropogenic effects on aphid biology

Autumn daily minimum temperatures in coastal eastern Australia are probably higher than the temperatures in the east-Asian countries of origin of *S. kahawaluokalani*, *S. celtis* and *T. ulmiparvifoliae* and are likely to increase with climate change. The cold threshold for induction of sexual forms may not be reached, leading eventually to continuous anholocyclic reproduction, provided that at least part of the population can survive the winter. Higher autumn temperatures may disrupt the complex of events that allow an aphid population to produce overwintering eggs and, if accompanied by low winter temperatures, could compromise its local survival if no food source is available, e.g. for aphids dependant on fully deciduous trees. Clones that are already anholocyclic outcompete holocyclic populations. The "cost of sex" in aphids has been widely discussed: see for example Simon *et al*. (2002).

In this study area, daily maximum temperature was as high as 47 °C in January 2020, 44 °C in February, 37 °C in March and 30 °C in April. These high temperatures could cause direct mortality of both aphids and host plants, thus reducing diversity of species in the area. It is suggested that these high temperatures caused reduction of *Tuberculatus annulatus* in summer 2020. In coastal eastern Australia, minimum temperatures are not generally so low that aphids will be directly killed, so that anholocyclic reproduction can be maintained at a low level provided host plants remain. It would be interesting to compare annual cycles of aphids in the Sydney region with those in Armidale, Canberra or Orange, where winter temperatures are much colder. It is not clear whether the catastrophic bushfires of summer 2019-20, or the smoke they produced, might affect aphid populations generally associated with cultivated plants. Effects on survival and activity of predators and parasitoids are unknown, as are their consequent impact on aphid populations.

Scotoperiod is the other major determinant of sexual reproduction and it is relevant to consider how environmental artificial light at night may impinge on aphid annual cycles. This was studied experimentally by Sanders *et al*. (2015) and they showed that added artificial light did delay the onset of male production by the aphid *Megoura viciae* Buckton.

Geographic changes in aphid diversity

Bell *et al*. (2015) used 50 years of data from the Rothamsted Insect Survey (RIS) suction trap network to show changes in spring and autumn flight times of 55 holocyclic aphid species in Europe, with both flight periods becoming earlier in many species. Leather (2015), discussing the paper by Bell *et al*., noted that "crop pests and pathogens have, over the last 50 years, been moving polewards", which will alter the pest profile on particular crops. Further, some pests may be becoming less common. The RIS trap array continues to collect species new to the trap locations.

The single set of observations in the current paper is a snapshot in comparison with the continuous and multi-locus records of the RIS, but provides some suggestive parallels. Some aphids that were commonly found in Sydney in the 1960s are now not often seen, while species not known in Sydney (or Australia) in the 1960s are now common. There is a tendency towards anholocycly. The shifts in distribution observed by Bell *et al*. (2015) could well apply in Australia, with a possible movement of mainland species towards southern states, and invasion of new species from Asia and elsewhere. Clearly, more comprehensive longitudinal studies of aphid numbers, species distribution, annual cycles and changes in pest status in the Southern Hemisphere generally, and Australia, in particular, would be valuable.

overflow during rain, and I thank him again for his continuing support of my aphid projects.

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