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Rediscovery of the Desert Sand-skipper *Croitana aestiva* Edwards (Lepidoptera: Hesperiidae): morphology, life history and behaviour

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Abstract *Croitana aestiva* Edwards is one of Australia's most poorly known butterflies. Previously it was known from a total of eight specimens collected in 1966 and 1972 in the MacDonnell Ranges west of Alice Springs in central Australia. The species was not positively recorded for the next 35 years; however, in February 2007 a population was rediscovered during targeted surveys. Subsequent biological studies were conducted from 2007 to 2010. A reappraisal of adult morphology show that four character states are unique to *C. aestiva*. Eggs are creamy-white and subcircular, with 21–29 longitudinal ribs. First-instar larvae are creamy-white, with a dark head capsule and prothoracic plate. Fourth- and fifth-instar larvae have a dark green medial band, a pale lateral band on each side of the body, and a distinct, highly setose, brown anal plate. The pupae are mainly orange-brown, darkening anteriorly, with a highly sculptured pupal cap. The larval food plant is the grass *Neurachne tenuifolia* (Poaceae), which is also endemic to central Australia. Shelters for all larvae and the pupa are among the leaf sheaths and stems near the base of the tussock. Adults are opportunistic feeders on a wide variety of nectar-producing plants, and are active throughout the day. Males use patrolling and perching behaviour to locate receptive females at a range of encounter sites, including the larval food plant and hilltops. Oviposition occurs during late morning, and eggs are laid on the upper surface of blades of the food plant. Comparison of the immature stages of *C. aestiva* with its congeners indicates many similarities in general morphology, but there are pronounced behavioural differences such as upward-orientated shelters.

Key words arid zone, butterfly, central Australia, ecology, immature stages, mate-location behaviour.

INTRODUCTION

The genus *Croitana* Waterhouse (Lepidoptera: Hesperiidae: Trapezitinae) comprises three described species endemic to Australia (Edwards 1979; Braby 2000). The Yellow Sand-skipper *C. croites* (Hewitson) is restricted to Western Australia, where a 'pale form' is found in central western areas, and a 'dark form' is found in the south-west near Perth (Graham 1988; Braby 2000). The Inland Sand-skipper *C. arenaria* Edwards currently comprises two subspecies: *C. arenaria arenaria* Edwards occurs in south-central parts of the Northern Territory (Edwards 1979) and northern South Australia (Grund & Hunt 2001), and *C. arenaria pilepudla* Grund occurs on the Eyre Peninsula of South Australia (Moore 1988; Grund 1999, 2003). The third species, the Desert Sand-skipper *C. aestiva* Edwards, the subject of this paper, is known only from a limited area in the southern Northern Territory. Biogeographically, the genus is remarkable as it represents the only lineage of Australian butterflies that has radiated into arid and semi-arid biomes. The larval food plants, life history and other aspects of the biology of *C. croites* and *C. arenaria* are well-known: those of *C. croites* were described by Graham (1988), those of *C. arenaria arenaria* were described by Atkins and Miller (1987) and Grund and Hunt (2001), whereas those of *C. arenaria pilepudla* were described by Grund (1999) and Grund and Hunt (2001). The immature stages and life history of *C. aestiva*, however, have remained unknown; in fact this skipper represents the only one of the 71 described species of Australian Trapezitinae for which the larval food plant has not been reported.

The first adult specimens of *C. aestiva* were collected in February 1966 from two localities in central Australia: along a roadside 25 km west of Alice Springs, and at Standley Chasm, 41 km west of Alice Springs (Edwards 1979). A second series of specimens was collected in April 1972 at Ellery Creek Big Hole, 82 km west of Alice Springs (Braby 2000). Despite several entomologists searching the type localities and nearby areas over a number of years the species had not been recorded since 1972 and was thought to be declining or possibly extinct.

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This led to the listing of the species as 'Endangered' under Northern Territory and Commonwealth legislation. In February 2007 a population was re-discovered during targeted surveys at Standley Chasm by CMP, and studies were conducted from 2007 to 2010 to determine further aspects of its morphology, biology and conservation status. In this paper we present the results of some of this research, including a reappraisal of adult morphology, description of the life history, and the behaviour and ecology of adults and immature stages. A forthcoming paper will describe the species' distribution and phenology, and assess its conservation status and management (Palmer 2010).

MATERIALS AND METHODS

Taxonomic reassessment of adults

Edwards (1979) described *C. aestiva* based on six specimens in the Australian National Insect Collection (ANIC): the holotype male; four paratype males; and a paratype female, all collected in 1966. The additional specimens collected in 1972 comprise two worn specimens in poor condition in the Northern Territory Economic Insect Collection (NTEIC). Thus, prior to this study, the entire known collection of *C. aestiva* consisted of only six males and two females. Edwards (1979) provided a detailed description of the species, gave comparative notes on variation and differences among the sexes, and drew attention to diagnostic features.

Rediscovery of the species provided the opportunity to obtain additional material, currently housed in the Museum and Art Gallery of the Northern Territory (NTM), and build on the taxonomic foundation laid down by Edwards (1979). Specifically, we reassess morphological variation within the species, compare character differences between the sexes and between related species, and comment on unique character states by which the taxon may be diagnosed. Of the additional material collected, sixteen males and twenty females in good condition were available for study.

Descriptions of immature stages and maintenance of developing eggs

Developing eggs, while still attached to pieces of leaves, were measured using a dissecting microscope with an eyepiece graticule. Larvae and one pupa were preserved in 70–80% ethanol before measurement.

To facilitate egg development ~50 mm pieces of grass blade, each with attached egg, were excised from plants and placed individually in plastic specimen jars with small air holes in the lids. A small ball of moistened cotton wool was pushed onto one end of the blade to keep the grass as fresh as possible. Eggs were kept in a room well-lit by natural light and exposed to natural diurnal changes in light conditions. Eggs were maintained at 22–28°C, and their development monitored every 24 h until eclosion.

Observations of adult behaviour

Most of the general field observations of adults and immatures presented in this paper were conducted at Standley Chasm (23°43'S, 133°28'E), although some results such as the diversity of nectar-producing plants visited by adults are collated from other locations sampled over the last three years.

To ascertain if adult nectar feeding occurred at particular times of the day, feeding frequency was observed at two sites 400 m apart at Standley Chasm. The only species flowering at each site was the sunflower daisy *Wedelia stirlingii* (Asteraceae). Site 1 was approximately 28 m^2, and contained 13 plants of *W. stirlingii* covering an area of approximately 5.5 m^2. This site was located on flat ground, beside the stony headwaters of a narrow creek, with numerous shrubs and trees providing shelter throughout much of the day. Site 2 was approximately 32 m^2, and contained 11 plants covering an area of approximately 6.5 m^2. This site was located on an open, exposed, steeply sloping hillside without an overstorey. Data comprised counts of the maximum number of adults observed feeding throughout each site over a two-minute period, initially at half hourly intervals (from 0830 to 1030 h) and then hourly intervals (1030 to 1730 h).

For field observations of mate location and encounter sites many individuals in the breeding areas were captured and released or observed perching at very close distances to determine their sex.

RESULTS

Croitana aestiva Edwards, 1979

Taxonomic reassessment of adults

Material examined

1♂, 1♀ labelled 'Ellery Gorge via Alice Springs, NT, 15.iv.1972, T. Weir & T. Angeles' (NTEIC); 4♂, 3♀ labelled '23°43.041'S, 133°28.220'E, Standley Chasm, NT, 15 FEB. 2007, C.M. Palmer, sweep net' (NTM); 1♂, 2♀ labelled similarly but with date '22 FEB. 2007' (NTM); 1♂, 2♀ labelled '23.72150°S, 133.46982°E, Standley Chasm, West Macdonnell Ranges, NT, 1 MAR. 2007, M.F. Braby & C. Palmer' (NTM); 2♂, 3♀ labelled similarly but with date '2 MAR. 2007' (NTM); 1♂, 1♀ labelled similarly but with date '3 MAR. 2007' (NTM); 2♂, 4♀ labelled similarly but with date and collector '23 APR. 2007, C. Palmer' (NTM); 5♂, 6♀ labelled '23.71613°S, 133.46925°E, Larapinta Trail, Standley Chasm, NT, 12 FEB. 2010, 850 m, M.F. Braby & C. Palmer' (NTM); 6♀ labelled similarly but with date and collector '14 FEB. 2010, M.F. Braby & L.J. Aitchison' (NTM).

Morphological variation

Edwards (1979) noted that males exhibit slight variation in the size of the postmedian and subterminal spots on the upperside

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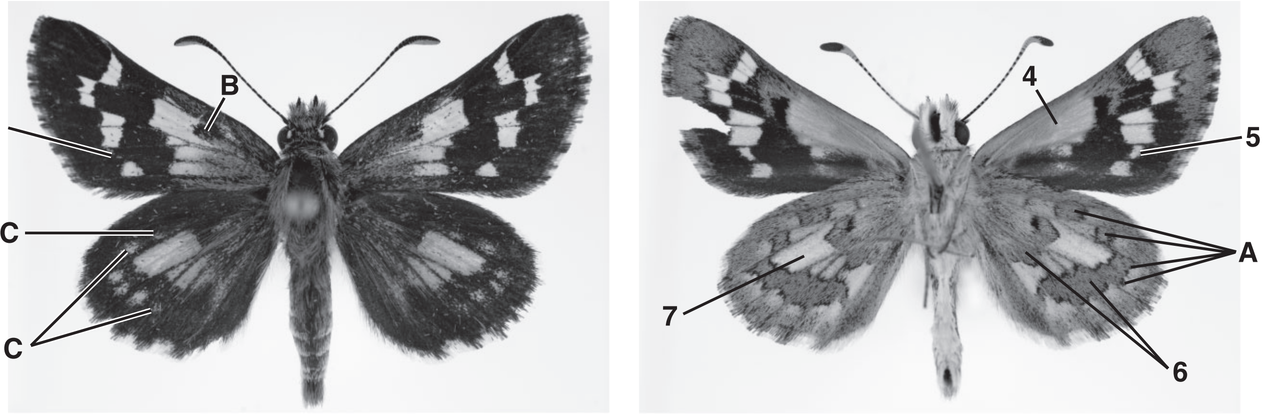

Figs 1&2. *Croitana aestiva*, male, showing morphological features referred to in the text. (**1**) Dorsal view. (**2**)Ventral view. Numbers 1–7 refer to characters in the section 'Morphological variation', and letters A–C refer to characters in the section 'Diagnosis'.

of the forewing. Examination of new material has revealed seven additional characters by which the species varies (numbered 1–7 in Figs 1,2; see also Figs 3–10). These characters include:

1 Presence/absence of an additional pale yellow postmedian spot between veins CuA$_2$ and 1A+2A on the upperside of the forewing (Figs 1,5,6,8–11). In most specimens there is only one spot, which is well separated from the two pale yellow postmedian spots between veins M$_3$ and CuA$_2$, but in some specimens (♂ 19%, ♀ 70%) there is a second anterior spot or narrow streak connected to these two spots forming a confluent band of spots from M$_3$ to 1A+2A.

2 Presence/absence of dark yellow subterminal spots on the upperside of the hindwing (Figs 1,4). A small proportion of specimens (♂ 31%, ♀ 5%) have a series of up to five small spots between veins Rs and CuA$_2$; when present the spots are usually obscure and may be reduced to a few inconspicuous dark yellow scales.

3 Presence/absence of a small obscure dark yellow postmedian spot between veins Rs and M$_1$ on the upperside of the hindwing (Figs 1,3,4,6–8). A proportion of specimens (♂ 31%, ♀ 35%) have this spot, which occurs adjacent to the large elongated dark yellow spot between veins M$_1$ and M$_3$.

4 Presence/absence of an obscure black spot within a dark yellow area in the discal cell on the underside of the forewing (Figs 2,3,5,7–10). This spot when present (♂ 62%, ♀ 100%) also varies in extent.

5 Presence/absence of an additional yellow postmedian spot between veins CuA$_2$ and 1A+2A on the underside of the forewing (Figs 2,5,6,8–10). In most specimens there is only one spot, which is well separated from the two paler yellow postmedian spots between veins M$_3$ and CuA$_2$, but in a small proportion of specimens (♂ 12%, ♀ 25%) there is a second anterior spot or streak that is confluent with these two postmedian spots.

6 Variation in colour of the submedian and postmedian bands of spots on the underside of the hindwing (Fig. 2). In females, the spots vary from pale yellow-brown to dark brown so that the clarity of the spots may be either obscure (Fig. 9) or more prominent (Fig. 7) against the underside ground colour.

7 Variation in colour of the large elongated spot between veins M$_1$ and M$_3$ on the underside of the hindwing (Fig. 2). The spot is frequently pale yellow-brown and inconspicuous, but in many specimens (♂ 62%, ♀ 33%) it is pale yellow and highly conspicuous against the darker ground colour (Figs 3,4,6).

Sexual dimorphism

Edwards (1979) remarked that the sexes differ in wing shape, with the female having narrower wings and the termen more rounded than the male; in wing length, with the female having longer wings; and in the pattern of the dark yellow area in the discal cell on the underside of the forewing, with a black spot present in the female but not in the male. Comparison of a larger series of specimens revealed that although females have the termen of the hindwing more rounded, they did not differ appreciably in overall wing shape (i.e. width). However, measurements made on wingspan (i.e. straight line distance between the apex of each forewing) of correctly spread specimens revealed that females ($\bar{x} = 26.94 \pm 1.117\,\mathrm{SD}$, range 24.9–28.8, $n = 18$) were significantly larger than males ($\bar{x} = 24.39 \pm 1.120\,\mathrm{SD}$, range 22.8–26.10, $n = 14$) ($t = 6.42$, 30 d.f., $P < 0.0001$). The presence of an obscure black spot in the discal cell on the underside of the forewing was found to be an unreliable character by which to distinguish the sexes. Although this character was present in all females, it was also present in almost two thirds of all males examined.

Three additional characters were found to separate the sexes, including differences in the intensity and extent of yellow spots and patches on the upperside, in the colour and clarity of the submedian and postmedian bands of spots on the underside of the hindwing, and in the size and shape of the abdomen. In the female (Figs 7–11), the yellow spots and patches on the upperside are less extensive, especially the submedian patch in the

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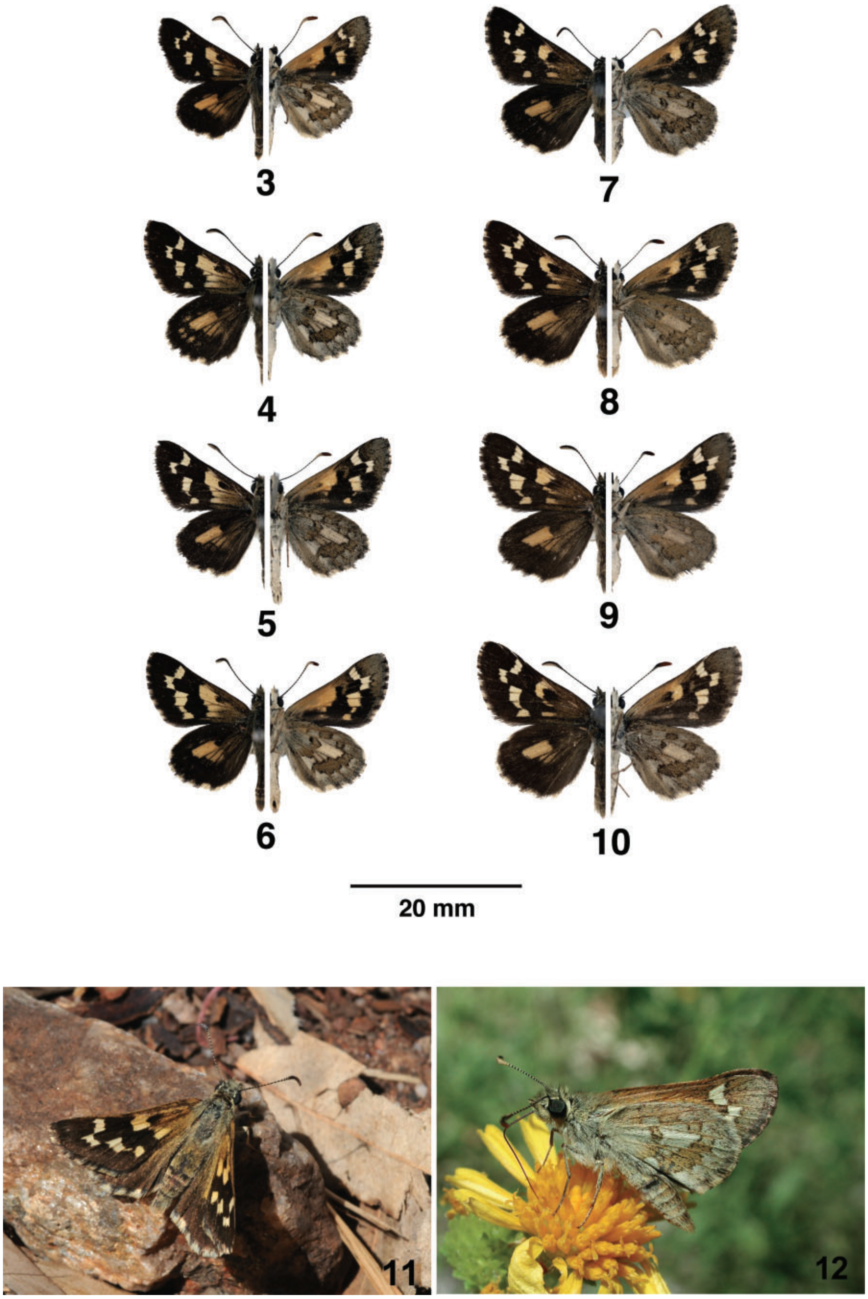


Figs 3–12. Adults of *Croitana aestiva*. (**3–6**) Males showing morphological variation. (**7–10**) Females showing morphological variation. For each specimen in Figure 3–10, the dorsal view is shown on the left and the ventral view on the right. (**11**) Female basking during early morning. (**12**) Male feeding from *Wedelia stirlingii*. Photos 11–12 by M.F. Braby.

discal cell and adjacent areas between the cubitus and anal veins of the forewing, compared with the male; the spots are also somewhat duller in the female. In the male (Figs 3–6,12), the submedian and postmedian bands of spots on the underside of the hindwing are consistently darker yellow-brown and conspicuous against the underside ground colour, whereas in the female this character is more variable in colour and the spots are generally more obscure. The abdomen is broader and less tapered posteriorly in the female than in the male.

Diagnosis

Edwards (1979) listed a number of taxonomic characters to separate *C. aestiva* from *C. arenaria* and *C. croites*. However, consideration of the morphological variation within and among the sexes of *C. aestiva* has necessitated a review of the characters by which the species may be diagnosed against its congeners. Five diagnostic characters listed by Edwards (1979) – wing shape, pattern of dark yellow central patch on the upperside of the hindwing, degree of difference in colour of spots between fore- and hindwings, pattern of cilia, and antennal morphology – were found to be not applicable because the states are shared with the related species. The wing shape of *C. aestiva* has been considered to be narrower than the two other species; however, this state was based largely on the single paratype female that, although having narrower forewings, is not typical of the species. In *C. aestiva*, the dark yellow central patch on the upperside of the hindwing is divided by dark brown veins. Although this character state is not shared with *C. arenaria arenaria* or *C. croites* it does occur in the subspecies *C. arenaria pilepudla* from the Eyre Peninsula (Grund 2003, 2009). Edwards (1979) noted that the yellow spots on the forewing are similar in colour to the central patch on the upperside of the hindwing. Comparison of fresh material, however, indicates that the yellow spots on the forewing are generally paler yellow than the central patch on the hindwing, which is dark yellow, although the degree of difference is not as pronounced as in *C. arenaria arenaria* or *C. arenaria pilepudla*. Furthermore, in *C. croites* 'dark form' the yellow spots on the fore- and hindwings are identical in colour. Edwards (1979) also noted that the cilia of the wings (i.e. scale fringe) in *C. aestiva* is uniformly coloured or faintly chequered compared with *C. arenaria arenaria*. However, examination of fresh material revealed that the cilia on the upperside is conspicuously chequered dark brown and pale brown, whereas that on the underside of the forewing is chequered dark brown and pale yellow. The number of nudum segments on the antennal shaft varies from 13 to 14 in *C. aestiva*, whereas there are 12 in *C. arenaria arenaria* and 12–13 in *C. croites* (Edwards 1979); however, the range overlaps with that recorded for *C. arenaria pilepudla* (12–14) (Grund 2003, 2009). Edwards (1979) remarked that in *C. aestiva* the antennal shaft broadens gradually into the club, whereas the shaft in *C. arenaria* and *C. croites* joins more abruptly with the club. However, we consider this character to be too subjective to warrant further consideration.

The following four character states are considered to be unique to *C. aestiva* (the first three shown as A–C in Figs 1,2), although it has not been ascertained if they comprise autapomorphies or plesiomorphies:

A *Submedian and postmedian bands of spots on underside of hindwing dark yellow-brown, with spots between veins Sc+R$_1$ and Rs, and veins Rs and M$_1$ well separated from the other postmedian spots and those between veins M$_1$ and M$_3$ narrower than the adjoining postmedian spots*: In *C. aestiva*, the arrangement of the bands of spots is similar to that in *C. croites*; however, in *C. croites* these spots are dark yellowish-grey or orange-brown. The colour of the spots in *C. aestiva* is similar to that in *C. arenaria arenaria* in being yellow-brown, but in the latter species the spots form broad submedian and subterminal bands, with those spots between veins Sc+R$_1$ and Rs and between veins Rs and M$_1$ confluent with the postmedian band and those spots between veins M$_1$ and M$_3$ broader and extending distally to the termen. Thus, the combination of pattern and colour of the bands of spots on the underside of the hindwing is diagnostic in *C. aestiva*.

B *Presence of dark brown submedian spot in discal cell on upperside of forewing*: In both sexes of *C. aestiva*, the proximal edge of the large pale yellow patch in the discal cell and adjacent pale yellow spots between veins Cu and 1A+2A on the forewing frequently partly encloses a conspicuous circular or elongated dark brown spot devoid of yellow scales; this spot is absent in males of both *C. arenaria arenaria, C. arenaria pilepudla* and *C. croites* and is usually absent in females of these species (when present it is very poorly developed).

C *Presence of small dark yellow subterminal and postmedian spots on upperside of hindwing*: This character state is present in only a small proportion (16%) of all specimens examined ($n = 36$) and therefore hardly diagnostic, but it appears to be unique to *C. aestiva*.

D *Tip of ampulla narrow and strongly curved inwards*: Edwards (1979) illustrated a number of differences in the male genitalia between the three species, including the shape of the ampulla on the valva, the tip of which in the other species is broader and less curved (*C. croites*) or not curved at all (*C. arenaria arenaria*).

Morphology of immature stages

Egg (Figs 13–15)

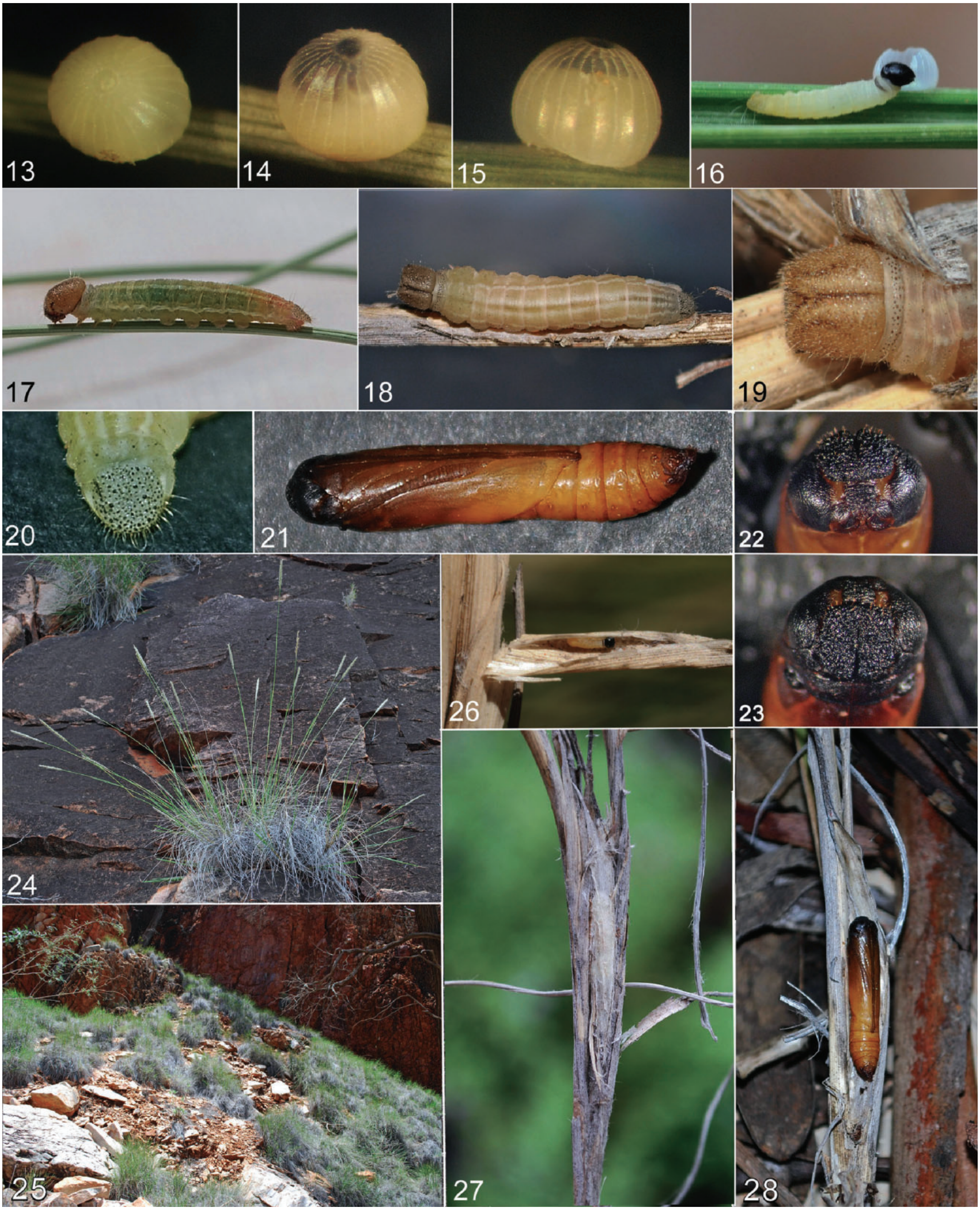
Width 1.18–1.40 mm, length 1.31–1.52 mm at greatest dimensions; subcircular to suboval in dorsal view, dome-shaped in lateral view, base flattened, though following curvature of leaf blade; creamy-white; surface with 21–29 longitudinal ribs usually extending from micropylar depression to base, though some ribs fork and others peter out below micropyle; each rib connected to adjacent ones by very fine transverse ridges.

First-instar larva (Fig. 16)

Body length 3.93–4.42 mm; head capsule width 0.65–0.74 mm; head very dark brown, shallowly pitted, with three anterior and two ventrolateral stemmata; head bears eight very prominent, pigmented, primary setae and numerous shorter setae. Prothorax bearing one, lateral, prominent primary seta on each side; prothoracic plate brown, with generally eight setae of different lengths, other setal sockets also sometimes present. Body creamy white; meso- and metathoracic segments and abdominal segments 1–9 bearing several short setae distributed dorsally and laterally; dorsal surface of segment 9 bearing two very prominent, pigmented, primary setae, and one pair of shorter, prominent, lateromedial setae; distinct anal plate of later instars not developed; segment 10 bears four very prominent, pigmented, primary setae, two posteriorly projecting, prominent, shorter setae, and two shorter, prominent, lateromedial setae; numerous other short setae also present.

Fourth-instar larva (Fig. 17)

Body length 11.0–17.5 mm depending on amount of feeding following diapause; head capsule width 1.71–2.00 mm; head brown, paler laterally; median adfrontal suture dark brown, a dark brown band either side of suture, extending anteriorly; covered with numerous shallow, irregularly shaped pits; arrangement of stemmata as for first instar; head covered with primary, secondary and short setae. Body generally creamy white, turning green on feeding, except for the following markings: dorsal surface of all body segments from



Figs 13–28. Life history of *Croitana aestiva*. (**13**) Egg, dorsal view. (**14**) Egg with developing larva visible. (**15**) Egg, lateral view, with developing larva visible. (**16**) Newly eclosed first-instar larva and partially eaten egg. (**17**) Fourth-instar larva, lateral view. (**18**) Fifth-instar larva, dorsal view. (**19**) Head, fifth-instar larva, dorsal view. (**20**) Anal plate, fifth-instar larva, posterodorsal view. (**21**) Pupa, ventrolateral view. (**22**) Pupal cap, anteroventral view. (**23**) Pupal cap, anterodorsal view. (**24**) Larval food plant *Neurachne tenuifolia*. (**25**) Typical breeding habitat, showing *N. tenuifolia* as the locally dominant species in the herb layer. (**26**) Shelter of first-instar larva at base of tussock, basal leaf sheath pulled away to expose larva. (**27**) Intact shelter of fifth-instar larva. (**28**) Pupa *in situ*, one side of shelter pulled away.

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mesothorax to anal plate bearing continuous, dark green, median band bordered by creamy-white band on each side; same body segments also bearing a pair of continuous, creamy white, lateromedial bands bordered by less pronounced darker green areas. All thoracic and abdominal segments bear circular, pigmented, non-setose, sensory discs. Prothorax bearing one, lateral, prominent, primary seta on each side; prothoracic plate pale brown, with numerous setae of different lengths; setal sockets very dark, distinct. Other thoracic and abdominal segments 1–9 bearing numerous shorter setae of different lengths, especially on dorsal and lateral surfaces, generally arranged in rows; arrangement of larger setae on segment 9 as for first instar. Anal plate distinct, pale brown, bearing numerous posteriorly projecting, primary setae and numerous shorter setae; setal sockets very dark, distinct.

Fifth-instar larva (Figs 18–20)

Body length 16.0–21.5 mm depending on amount of feeding; head capsule width 2.43–2.74 mm; head (Fig. 19) of identical colour and punctuation and as highly setose as fourth instar; arrangement of stemmata as for other instars. Sensory discs on all thoracic and abdominal segments as for fourth instar. Prothorax as for fourth instar. General body colouration and patterning as for instar IV; meso- and metathoracic segments and abdominal segments 1–9 also bearing numerous shorter setae generally in rows, although their sockets are darker and more distinct than in fourth instar; arrangement of larger setae on segment 9 as for other instars. Anal plate (Fig. 20) as for fourth instar, though setal sockets even darker, more distinct.

Pupa (Figs 21–23,28)

Length 16.0 mm (male); body slender, cylindrical; much of body orange-brown, darkening anteriorly and posteriorly so that mesothorax, basal part of forewing, anal area and cremaster are dark brown; antennae and proboscis also dark brown; prothorax and head very dark brown. Pupal cap (Figs 22,23) black; heavily sculptured, with rugose anterodorsal extension covered with bifurcate and trifurcate setae in moderate density, with deep median and shallower transverse furrows so that rugose extension appears divided into quarters; each dorsal quarter with a pair of ocelli. Proboscis extending ventrally past forewings, and just past junction of abdominal segments 4 and 5. Prothorax with a pair of small, pale, lateral spiracles. Anterior margin of mesothorax with a pair of dark, dorsolateral, rounded lobes, paler anteriorly. Abdominal segments with numerous, small, shallow pits, and sparsely covered with short setae. Spiracles on abdominal segments 2–7 oval, spiracle on segment 8 narrower, all pale orange-brown. Cremaster with a pair of short, pointed, ventrolateral projections; cremastral tip covered with numerous inwardly curved, spatulate, hooked setae; remainder of cremaster with short, widely spaced setae, especially on dorsal surface.

Life history and behaviour

Larval food plant and larval shelters

Larvae are monophagous on *Neurachne tenuifolia* S.T. Blake (Poaceae), a grass endemic to the West MacDonnell Ranges and adjacent areas in the southern Northern Territory. This grass has a tufted habit, reaching 300–500 mm in height, with long (80–250 mm), filiform, narrow (0.8–1.5 mm), rigid leaf blades with convolute margins (Sharp & Simon 2002). The base of mature tussocks is very dense with old and new growth of leaves (Fig. 24). The grass is generally found in sheltered rocky gullies and gorges and on steep, south facing, rocky slopes. It tends to be locally dominant in the most favourable habitats, and these constitute the main breeding areas of the butterfly (Fig. 25).

The shelters for all larvae and pupae are among the most basal, tightly wrapped, dry, broad leaf sheaths and stems near the base of the tussock. The first-instar larva shelters in the gap between the basal leaf sheath and stem (Fig. 26). Subsequent instars create shelters by joining basal leaf sheaths and occasionally bases of the narrow blades to the stem using silk. The fifth-instar larva has been found in a larger shelter comprising two stems and their basal leaf sheaths joined with silk (Fig. 27), although fifth-instar/pupal shelters have also been found comprising a stem and leaf sheaths (Fig. 28). All immature stages reside head upwards in their shelters.

Egg development and larval behaviour

Eggs hatched from 2 to 9 days after collection. Development was recorded for two eggs for which oviposition was observed, and the duration to eclosion was 8 and 9 days, respectively. The head capsule of the developing larva was visible 2 days before eclosion.

The chorion was wholly eaten by the first-instar larva immediately after hatching. In laboratory conditions eclosion and egg feeding always occurred overnight and were always completed by 0645 h, when observations began the following day. However, such behaviour also was observed on one occasion in the field during daylight, although the weather was cloudy, and observations were interrupted by heavy rain. On 12 February 2010, a hatching first-instar larva was first seen on a green leaf of the larval food plant at 1250 h, and began to eat the eggshell as soon as the head had emerged. It continued to eat the egg while the body was still partially inside, and when sufficient chorion had been consumed the larva stretched forward and deposited a small layer of silk on the leaf just distal to the egg. The larva crawled out, turned 180°, and used this silken platform to gain purchase while eating the remaining eggshell. The larva was fully eclosed at 1308 h. A heavy shower interrupted feeding at 1324 h, and the larva remained attached to the leaf in this position until observations ceased at 1350 h. The remnant chorion was still there the following day, and the larva was found at the base of the plant beneath the broad sheath enclosed tightly around the stem of a dry leaf.

In laboratory investigations using a potted larval food plant a newly eclosed first-instar larva was placed on a green leaf,

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and after 75 min of walking along the blades the larva was observed walking backwards down into the space created by the basal leaf sheath, approximately 25 mm from the soil surface. Further laboratory observations showed that larvae of all instars are able to walk backwards on grass blades, and usually retreated back into their shelters this way if disturbed. All larvae fed on the new growth of fresh blades, producing characteristic long (up to 52 mm for the fifth instar), narrow, serrated feeding marks on the leaves. Although signs of feeding were observed on many occasions, feeding never occurred during daylight, dusk or dawn. Despite attempts to rear larvae in captivity none survived development to the next stage.

Adult nectar feeding

Numerous adults, but mainly females, were observed feeding (e.g. Fig. 12) or attempting to feed throughout the day on a total of 14 species of nectar-producing plants (Table 1). Visits to two species (*Boerhavia coccinea*, Nyctaginaceae and *Jasminum calcarium*, Oleaceae) were very short (1–2 s); however, the proboscis was clearly extended in both cases, indicating attempts to feed.

Feeding activity generally followed the first appearance of sun on the flowers. Adults flew quickly and erratically between feeds, sometimes up to 9–10 m away, flying low to the ground or up in the canopy of small trees. They were also observed to fly several metres up and along rocky gorge walls and then down again to feed. Adults also had a short, bobbing flight between flowers where nectar plants were close together, often returning to the same plant or even the same flower. Observations showed that some plants were visited frequently, whereas others were not visited at all. Females sometimes opened and closed their wings while feeding, with slow fanning or wings held open to 45°. Males, and especially females, also often were observed alighting on leaf litter, rocks, plant stems, stones or twigs between feeding episodes, sometimes basking with wings open up to 90° (e.g. Fig. 11).

Between approximately 1400 and 1730 h female activity was often dominated by feeding and perching, particularly when there was prolific flowering of *Wedelia stirlingii*. During these times there was often almost no interaction between conspecific adults or with adults of different species as they alighted on flowers or when flying between flowers. At other times, adults were more easily disturbed during feeding, and always moved away when another, larger butterfly species alighted on the same or a nearby flower. When feeding males were disturbed or challenged by another male, the two engaged in an upward, rapid, spiralling flight for up to a metre before one or both dropped away and returned to feed.

Feeding occurred throughout much of the day at both survey sites (Table 2). The earliest time that adults were observed feeding was at 0830 h, and the latest at 1730 h (Table 2); however, three adults were also observed feeding elsewhere on *W. stirlingii* at 1817 h on 1 March 2007. Although feeding was not observed before 1000 h at Site 1 when conditions were shady, it was observed from 0830 h at Site 2 during sunny conditions. There were noticeably fewer observations of feeding at 1130 and 1230 h at Site 1, and slightly fewer observations at these times at Site 2. Feeding was not observed during early to mid afternoon (1330–1430 h) at the exposed Site 2. Feeding was observed in late afternoon full shade at both sites. During the morning (0900–1000 h) only females were observed feeding on flowers at Standley Chasm.

Table 1 Nectar-producing plants visited by adults of *Croitana aestiva*

Taxon	Colour of flowers visited
Amaranthaceae	
Ptilotus incanus	Pink
P. macrocephalus (Large green pussytail)	Yellowish-green
Apocynaceae	
Sarcostemma viminale (Caustic bush)	Pale green
Asteraceae	
Brachycome ciliaris (Variable daisy)	White
Wedelia stirlingii (Sunflower daisy)	Yellow
Boraginacaeae	
Trichodesma zeylanicum (Cattle bush)	Sky blue
Dilleniaceae	
Hibbertia glaberrima (Guinea flower)	Yellow
Fabaceae	
Glycine sp.	Purplish-pink
Goodeniaceae	
Goodenia grandiflora (Mountain primrose)	Mauve
Malvaceae	
Sida sp.	Yellow
Myrtaceae	
Melaleuca faucicola	Cream
Nyctaginaceae	
Boerhavia coccinea (Tar vine)	Purplish-pink
Oleaceae	
Jasminum calcarium (Poison creeper)	White
Solanaceae	
Solanum ellipticum (Potato bush)	Purple

Colour of flowers visited is noted because of the variability in flower colour of some species.

Mate location and encounter sites

Males were very active from 1030–1130 h on 14 February 2010, with peak activity between 1045 and 1115 h. During this time they patrolled rapidly close to the ground and around tussocks of the larval food plant in search of females, occasionally stopping to settle on rocks to bask for short periods (15–30 s). Very few males were observed in the breeding habitat outside these times. No males were seen in the breeding area before 1030 h and very few were seen between 1130 h and 1230 h; those that were observed after 1130 h were apparently just flying through the habitat, perhaps to nectar sources. Mating was not observed, but at 1102 h on 23 April 2007, a male and female were observed perching on the same stick before the pair flew off erratically high up on the gorge wall and out of sight.

Males were also observed hilltopping, usually from 1300 to 1630 h, although one male was observed as early as 1130 h. Males were observed selecting the highest sites on ridges and

Table 2 Numbers of adults observed feeding at flowers of *Wedelia stirlingii* (Asteraceae) at two sites between 0830 and 1730 h. The symbol ☼ and degree of shading refer to full sun (white), part/dappled sun (pale grey), or full shade (dark grey). See text for more details

Time	Site 1								Site 2			
	22/2/07	1/3/07	2/3/07	6/3/07	7/1/09	8/1/09	Total	Sun/shade	11/1/09	12/1/09	Total	Sun/shade
0830	0	0	0	0	0	0	0	☼	1	2	3	☼
0900	0	0	0	0	0	0	0	☼	3	2	5	☼
0930	0	0	0	0	0	0	0	☼	2	2	4	☼
1000	1	2	2	2	1	1	9	☼	2	2	4	☼
1030	3	2	3	1	1	2	12	☼	3	3	6	☼
1130	1	1	0	1	3	1	7	☼	2	0	2	☼
1230	1	0	0	0	3	3	7	☼	2	1	3	☼
1330	0	1	0	1	4	5	11	☼	0	0	0	☼
1430	1	2	1	0	5	3	12	☼	0	0	0	☼
1530	2	0	0	1	4	3	10	☼	2	3	5	☼
1630	1	1	2	0	3	3	10	☼	2	1	3	☼
1730	3	1	1	1	2	2	10	☼	2	2	4	☼

small peaks just above the breeding habitat. They typically perched on rocks at the summit and were defending territories from conspecific males. Other perching sites observed included stones on the bare patches of walking tracks on the summit of hills, stems of non-larval food plant grasses (*Themeda* sp.), and dead, woody, defoliated stems of shrubs.

Observations of hilltopping behaviour of two males were made on 20 December 2008. The territory of one male was a level area approximately 2 m^2, and comprised predominantly bare rocks and stones separated by spinifex (*Triodia* sp.). The territory of the second male was a longer, narrower (but unmeasured) area. Neither territory contained nectar sources for the adults. Flights of both males occurred at intervals of 2–5 min, when: (1) one of the males instigated a flight and was then joined by the other; or (2) when another flying insect disturbed a perched male. One male would join the other as the territory boundary was crossed. Flights of both males were fast and erratic, occurring in a wide, circular pattern. After short bursts of flight (usually <10 s, occasionally longer) each male returned to his territory. Each male also flew separately to change perch within his territory. One of these males almost always faced the same direction when perching, which was towards the closest, descending slope. The abdomen was sometimes raised in perching males.

Oviposition behaviour

One female was observed to lay two eggs on 29 January 2010. Observations began when it landed on a green leaf blade of the larval food plant and immediately laid the first egg at 1112 h. The female then flew away briefly, slowly fluttering within 2 m of this plant before alighting on the same blade of grass and after three seconds laid a second egg at 1115 h. This female then flew erratically away much more quickly through the breeding area out of sight. The female's body was aligned along the axis of grass blade during oviposition.

Another two females were observed to oviposit on 14 February 2010. The first female was spotted whilst settling on a rock at 1130 h; at 1133 h it attempted to oviposit on an adjacent tussock of the larval food plant by alighting on the grass and curling the abdomen but no egg was laid. It then flew back to bask on the same rock. At 1135 h it repeated this process but again did not lay. The female then sat on another rock for 5 min and basked with wings open before flying to a nearby tussock and deposited an egg at 1140 h near the apex of a dead brown leaf. The second female was detected at 1135 h in the same breeding area. It perched for 15 mins on a dead stick on the ground in the shade, near a tussock of the larval food plant. At 1151 h it flew up to the tussock and laid a single egg on a green leaf, before flying away out of sight. No females were observed in the breeding habitat during the afternoon of 14 February 2010, other than those feeding from nectar of flowers. However, at 1435 h on 18 February 2010 a female was observed in the breeding area alighting on a food plant and curling the end of its abdomen downward but no egg was laid. The female flew off and landed on a nearby boulder, and at 1439 h it flew slowly back in a fluttering manner onto a different food plant, again curling the abdomen without oviposition. This female then flew away out of sight among other food plants in the breeding area. No other female activity was observed in the breeding area during that afternoon.

All eggs observed on the larval food plant were laid on the upper, convex surface of the leaf blade, and most were laid on fresh, green leaves, although a few eggs were observed on older, dry blades. Eggs were not distributed randomly on leaves ($\chi^2 = 99.617$, 200 d.f., $P < 0.0001$, $n = 37$), instead following a normal distribution (Kolmogorov–Smirnov Goodness of Fit $D = 0.161$, $P = 0.269$, alpha 0.05), with most laid around the mean distance from the apex of the blade ($\bar{x} = 72.73$ mm, SD = 39.260) (Fig. 29). There was no preference for certain individual larval food plants on which females oviposited ($\chi^2 = 7.815$, d.f. 3, $P < 0.001$, $n = 39$), with most eggs being laid on separate plants (Fig. 30).

Natural enemies

Predation of adults was observed on two occasions: on 7 March 2007 a female was being eaten by the fast-moving hunting spider *Oxyopes* sp. (Araneomorphae: Oxyopidae) (Fig. 31), and on 30 November 2007 a female was being eaten

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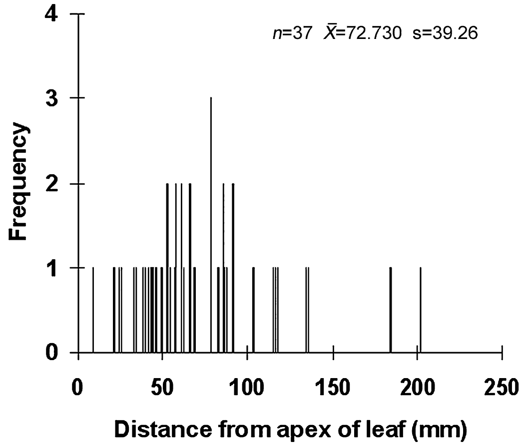

Fig. 29. Frequency distribution of distance of egg of *Croitana aestiva* from apex of blade of larval food plant.

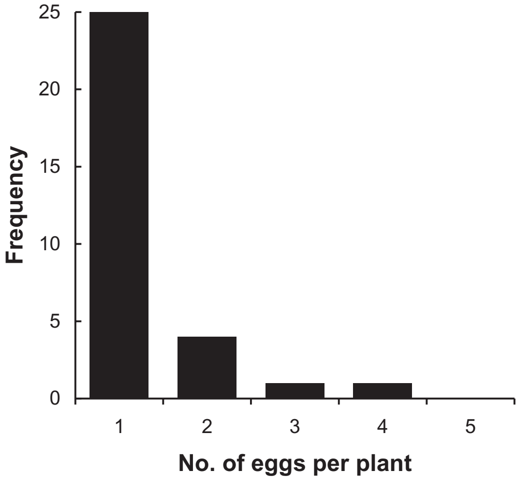

Fig. 30. Frequency distribution of number of eggs of C*roitana aestiva* on the larval food plant.

Fig. 31. Adult of *Croitana aestiva* caught by the hunting spider *Oxyopes* sp. (Araneomorphae: Oxyopidae). Photo by C.M. Palmer.

by the assassin bug *Poecilobdallus formosus* (Stål) (Hemiptera: Reduviidae). Numerous other potential predators, such as web-building spiders, praying mantids and lizards, were present in the breeding and foraging habitats, but no further instances of predation were recorded. Adults were observed escaping from the Long-nosed dragon *Lophognathus longirostris* (Boulenger) (Agamidae) on several occasions.

DISCUSSION

Taken together, results of observations of adult behaviour over the three years indicate the following temporal pattern of diurnal activity. During the morning, feeding by females occurs as soon as their body temperature is high enough for flight. Female feeding continues until mid to late morning, when males are most actively patrolling for receptive females in the breeding areas; mating most likely occurs soon afterwards. This is followed by oviposition during late morning in the breeding areas, which coincides with observed reductions in adult activity at flowers (Table 2). Thus, the timing of peak activity of the two sexes in the breeding areas is temporally separated, with that of females immediately following males.

During the afternoon, female behaviour is once more dominated by feeding, which continues until almost dusk. Males also feed and select and defend territories on hilltops from which to locate females. Males therefore use at least two encounter sites, and different behavioural strategies, to locate receptive females: the larval food plant, and non-resource based landmarks (hilltops). Patrolling is apparently limited to a narrow window during mid morning, whereas the extent of perching is less constrained temporally, occurring throughout much of the day. Males of the closely related genus *Herimosa* Atkins also patrol areas near the larval food plants for females (Atkins 1994). Hilltopping is a common feature of males of species in the Trapezitinae (Braby 2000), and Edwards (1979) reported males of *C. arenaria arenaria* defending territories in dry creek beds in the MacDonnell Ranges.

The alternative mate-location tactics of *C. aestiva* is one that is not present in most species of Trapezitinae (Braby 2000); however, males of the eastern Australian species *Trapezites symommus* Hübner also patrol only in the morning and then establish perch sites and defend territories in the afternoon by perching on the foliage of trees (Braby 2000).

There was no observed preference for any plant species or flower colour during feeding; adults fed apparently opportunistically on whichever species was flowering, and this varied

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Table 3 Comparison of the immature stages of *C. aestiva* with the published morphological and biological data of immatures of all other taxa of *Croitana*

Character	*C. aestiva*	*C. croites* 'pale form'	*C. croites* 'dark form'	*C. arenaria arenaria*	*C. arenaria pileludla*
Egg					
No. of longitudinal ribs	21–29	21	22	13–16	18–22
Larvae					
Instar I					
Colour of prothoracic plate	Brown	Dark brown	–	Black	–
Two primary setae on dorsum of seg 9	Present	Present	–	Not reported	–
Instar V					
Dark green median band on body	Present	Present	–	Present	–
Pair of pale, lateromedian bands on body	Present	Present	–	Present	–
Head shallowly pitted	Yes	Yes	–	–	–
Median adfrontal suture	Dark brown	Dark brown	–	–	–
Dark brown band either side of median adfrontal suture	Present	Present	–	Present	–
Colour of setal sockets on anal plate	Dark brown	Dark brown	–	–	–
Pupa					
Pupal cap extension	Rugose	Rugose	–	Rugose	Rugose
Transverse and median furrows	Present	Present	–	Present	Present
Cremaster with pair of ventrolateral projections	Present	Present	–	–	–
Larval food plant	*Neurachne tenuifolia*	*Austrostipa platychaeta*, *A. elegantissima*	*Austrostipa flavescens*	*Enteropogon acicularis*, *E. ramosus*	*Austrostipa platychaeta*, *A. elegantissima*
Oviposition site on larval food plant	Upper surface of leaf blade, nearer to apex	Upper surface of leaf blade, nearer to stem	–	Upper surface of leaf blade (position not reported)	Upper surface, usually in leaf axil
Feeding marks on leaves	Long, shallow, serrated	Short, deeper, 'wedge' shaped		Short, deeper, 'wedge' shaped	–
Shelter of instar I larva	Partly constructed (uses silk to help join basal leaf sheath and stem)	Constructed (by transverse folding of part of single leaf)	–	Constructed (by transverse folding of part of single leaf)	–
Shelter of instar V larva	Constructed from leaf sheaths and stems near base of tussock	Constructed from two or more leaf blades high up on plant	–	Constructed from two or more leaf blades high up on plant	–
Orientation of immature in shelter	Upward	Downward	–	Downward	–
Larval feeding	Nocturnal	Late afternoon & early morning	–	Dusk & dawn	Dusk

'–' refers to being not recorded or not reported. Published data from Atkins (1978), Atkins and Miller (1987), Graham (1988), Williams *et al*. (1997), Grund (1999), Braby (2000, 2004), Grund and Hunt (2001). Data for the pupa of *C. arenaria pilepudla* from unpublished photographs.

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throughout the season. The lack of visits to flowers of certain colours, such as red (see Table 1), only reflected the absence of such flowers at the sites where observations occurred. Where adults fed during the day depended on temperature and how exposed the flowers were to direct sun: flowers that were exposed for long periods including during the hottest part of the day were not as frequently visited, with adults instead feeding on flowers in shadier areas. Most trapezitine butterflies are active during periods of sunshine, often from late morning to early afternoon (Braby 2000). The continuous diurnal activity observed in *C. aestiva* (at least 0830 to1817 h) is likely to be an adaptation to the arid zone, taking advantage of a 'pulse' in resources following rain. Predation of a species of *Croitana* has not previously been reported; however, Atkins and Miller (1987) and Grund and Hunt (2001) observed mature larvae of *C. arenaria arenaria* being parasitised by small Hymenoptera, and Grund (1999) reported parasitisation of eggs of *C. arenaria pilepudla* by wasps and parasitisation of first- and second-instar larvae by Diptera.

Comparison of the immature stages of *C. aestiva* with the published morphological and biological data of the immatures of all other taxa of *Croitana* is shown in Table 3. Other than the reduced number of ribs on the egg of *C. arenaria arenaria*, much of the published general morphology of immatures is similar in all taxa. Future research should focus on a detailed comparison of the immature stages to highlight characters useful in differentiating the species and subspecies. Particular attention should be paid to the 'dark form' of *C. croites* and the subspecies *C. arenaria pilepudla*, of which there is little published information. The differences in larval food plant preferences within *C. arenaria*, together with adult morphological differences, indicate that the subspecies *C. arenaria pilepudla* is probably a separate species (Braby 2010). Investigating phylogenetic relationships based on morphological and molecular data would also test the monophyly and validity of all taxa in the *Proeidosa* group of genera as currently circumscribed (*sensu* Atkins 1994), as well as provide important insights into the biogeography of the arid zone (Byrne *et al.* 2008).

In most species in the subfamily Trapezitinae, eggs are deposited on the underside of the larval food plant leaf (Braby 2000); however, females of *Croitana* oviposit on the upper surface, although the position on the plant varies (Table 3). Laboratory and field observations indicate that eclosion of the first-instar larva is most likely nocturnal in normal circumstances, but may occur during the day depending on weather conditions. Unlike its congeners, larvae of *C. aestiva* do not construct shelters amongst the blades of grass, instead using the leaf sheaths and stems to construct a shelter near the base of the tussock. Also unlike its congeners, immatures of *C. aestiva* rest head upward in their shelters, and mature larvae construct shelters that open upward. This behavioural difference is most likely because the shelters are so low on the plants that access would be very difficult if they opened downward, and larvae were to enter head first. Narrowness of the leaves of the food plant also probably determines the morphology of the feeding marks: a large, growing fifth-instar larva requires significant amounts of food, and this can only be obtained with long, shallow feeding on a filiform leaf.

The presence of *C. aestiva* in central Australia raises questions as to how this interesting and remarkable species has adapted to the arid environment of low and unpredictable rainfall. Studies over several years indicate that adult activity is also very unpredictable, with the flight season finely tuned to these rainfall episodes. Preliminary field and laboratory observations indicate that the long and unpredictable dry spells are passed in the larval stage. Searches for the immature stages among the larval food plants and captive rearings suggest that this species aestivates for many months as a fifth-instar larva. In contrast, eggs, pupae or earlier instars were never recorded during dry periods, indicating that the final-larval instar is probably the only dormant stage for this species, as has been noted for *C. arenaria* (Grund & Hunt 2001). As the fifth instar is the largest of the immature stages it would also be the most resilient to long periods of drought that this species must endure on a regular basis. The physiological adaptation and tolerance to drought of the larval stage of *C. aestiva* and other members of the genus would make an interesting study.

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