Field observations of the Western Ring-tailed Rock Dragon, *Ctenophorus caudicinctus* (Günther, 1875)

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Abstract

An overview is presented of the behaviour and ecology of the common and visually prominent Western Ring-tailed Rock Dragon (*Ctenophorus caudicinctus*), based on field observations. Highlighted is the regional variation in the brightly coloured sexually dimorphic males in the northern part of its distribution (Pilbara) and the reduction in dimorphism in southern populations, including the Goldfields Ring-tailed Rock Dragon (*C. infans*).

Introduction

Storr (1967) recognised one species *Ctenophorus caudicinctus* (Günther) and seven subspecies of this saxicoline ring-tailed dragon lizard. The distinctions were based primarily on male colour (including if black caudal bands encircled the tail) and morphology (including the degree of lateral compression at the base of the tail). The subspecies were:

- *C. c. caudicinctus* found at the time throughout the Pilbara and some offshore islands in Western Australia (WA), from the De Grey River (although today it is known to extend much further northeast from near Anna Plains) south to the Hamersley, Ophthalmia and Robertson Ranges, although again today (*sensu* Storr) it has been observed south into the west Gascoyne to Williambury and the Kenneth Range (pers. obs.), and east to Well 24 on the Canning Stock Route;
- *C. c. graafi* in the central ranges of the eastern interior, southwest almost to Warburton, WA;
- *C. c. infans* in the eastern Murchison goldfields (eastern Goldfields) from northeast of Laverton south to near Kookynie;
- *C. c. macropus* in the Northern Territory (NT) near Oenpelli, although recently known to occur much more widely southeast into Queensland (Qld), and west into WA across the Kimberley;
- *C. c. mensarum* in the Murchison and eastern Murchison goldfields;
- *C. c. rufescens* in the far northwest of South Australia (SA), south to the Birksgate Range and east to Granite Downs;
- *C. c. slateri* in the southern highlands of NT from eastern Macdonnell Ranges southwest to the George Gill Range.

Distribution of the WA populations are shown in Figure 1.

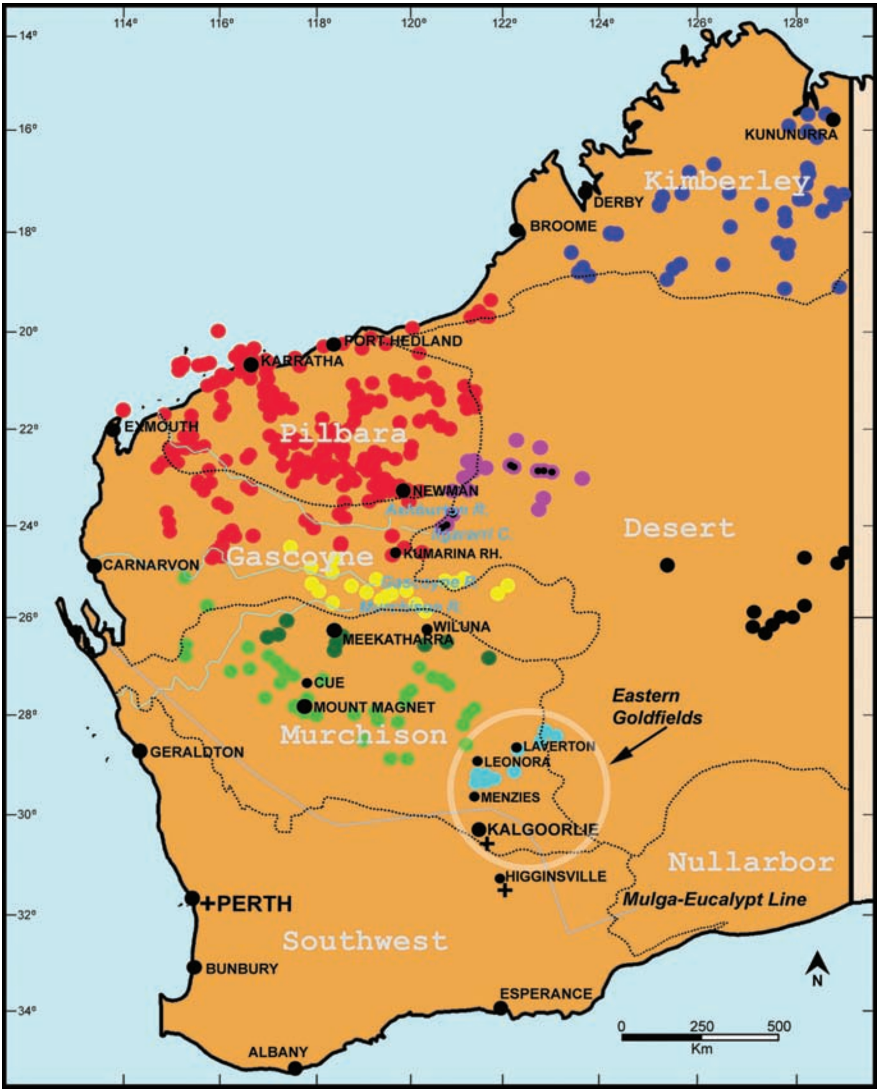

Figure 1. Map of Western Australia showing ring-tailed rock dragon distributions. Dark blue: *Ctenophorus slateri*; red: *C. caudicinctus* nominate population, greater Pilbara; mauve: *C. caudicinctus* eastern Pilbara (EP); mauve with black dot: EP *C. caudicinctus* sequenced by Melville *et al.* (2016); yellow: "*C. caudicinctus-mensarum* intergrade zone" (*sensu* Storr 1967); dark green: "*C. mensarum*" type series; pale green: southern *C. caudicinctus*; black: *C. graafi*; pale blue: *C. infans*; crosses: anomalous records of *C. caudicinctus* suspected of being inadvertently transported to each of the three locations (Perth, Boulder [near Kalgoorlie] and Higginsville).

Storr's 1967 inclusion of *Ctenophorus rufescens* (Stirling and Zietz) from the central ranges in eastern WA as a geographical race of *C. caudicinctus* was based on a lack of well-preserved specimens at the time. He remarked:

> "It is with some diffidence that I treat *rufescens* as a race of *caudicinctus*. For the scanty material is old or poorly preserved and, coming from widely separate localities, is highly variable. My main reasons for doing so are that *rufescens* is clearly a representative of *caudicinctus* and differs from other representatives in only two important respects; the numerous pores and the nostril located well below the sharp rostral ridge; but even these "key characters" are lacking in the single juvenile (SAM 1425)." (p. 52)

Today *C. rufescens* is excluded from the above group based on morphological and phylogenetic evidence and is now the western-most member of the *Ctenophorus decressii* (Duméril & Bibron) species group. The WA ring-tailed dragons, including *C. ornatus* (Gray) and *C. yinnietharra* (Storr), now form the *C. caudicinctus* - *C. ornatus* species group (Melville & Wilson 2019).

Based on both morphological and molecular evidence, Melville *et al.* (2016) recommended that *C. c. caudicinctus*, *C. c graafi* and *C. c. infans* be elevated to full species; *C. c. mensarum* be synonymised with *C. caudicinctus*, and that *C. c. macropus* be synonymised with *C. c. slateri*, elevating the latter to full species. Therefore, a recognition of four species: *C. caudicinctus*, *C. graafi*, *C. infans* and *C. slateri*. They acknowledged, however, that more work is required, particularly regarding *C. slateri* and *C. graafi*, including the relationship between the eastern populations of *C. caudicinctus* and *C. graafi*.

Excluding *C. graafi* and *C. slateri*, I will use Storr's western subspecies' distributions to separate the populations I am referring to from north to south as follows:

- Pilbara: *C. caudicinctus* - north to and including southwestern Kimberley;
- Central southern Gascoyne: "*C. caudicinctus-mensarum* intergrade zone" - immediately to the south of Ashburton River and Ilgararri Creek along latitude 25°S in the Gascoyne River floodplain;
- Northern Murchison: "*mensarum* type series" between latitudes 26°30'S and 26°51'S;
- Central Murchison: southern *C. caudicinctus* south of latitude 27°S.

This will allow the reader familiar with the older subspecies' names to quickly recognise the population in question as the field data and observations are presented, particularly on inter- and intrapopulation variation in adult males' colouration and size.

The Melville *et al.* (2016) study results in four species now occurring in WA with *C. caudicinctus* and *C. infans* endemic. The distribution of *C. caudicinctus* was enlarged with their synonymising of *C. mensarum* with it, such that *C. caudicinctus* now extends over much of the state from the southwest Kimberley in the north-eastern 80-Mile Beach area, south through the Pilbara and Gascoyne and into the greater Murchison and eastern Goldfields. In this paper I provide photographic examples of representatives from each population showing a north-south clinal change in colour and pattern (Figs. 2–5). Figure 6 also shows a corresponding reduction in size based on largest adult male and female snout-vent length (SVL) measured. Juvenile *C. caudicinctus* from the four respective populations are illustrated in Figure 7. The Pilbara *C. caudicinctus* juveniles look most like those from the "*C. caudicinctus-mensarum* intergrade zone" sharing a variable ground colour and simple body pattern, while the populations further south ("*C. mensarum* type series" and southern *caudicinctus*), including juvenile *C. infans* illustrated in Figure 8, share a

Figure 2. Variation in adult male *Ctenophorus caudicinctus* from the Pilbara. (A) Paraburdoo, (B) 32 km W of Pannawonica, (C) 38 km N of Munjina, (D) 36 km S of Karratha, (E) 35 km SE of Munjina Roadhouse, (F) Ord Ranges E of Pardoo Mine, (G) Karijini National Park, (H) 50 km E of Port Hedland. Photos: B. Bush.

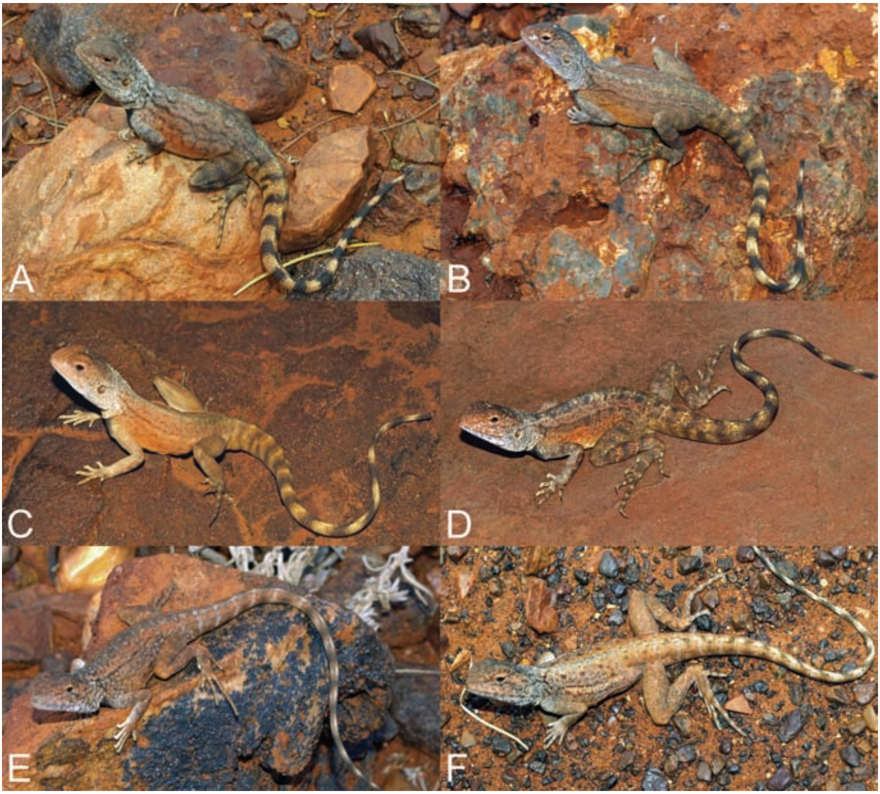

Figure 3. Variation in adult male ring-tailed rock dragons from the "*Ctenophorus caudicinctus-mensarum* intergrade zone" (*sensu* Storr 1967) in the central southern Gascoyne which is along the northern boundary of the "*C. mensarum* type series". The Three Rivers Station access road is 195 km N of Meekatharra and runs WNW of the Great Northern Highway. For a photo of the habitat along this road see Fig. 19C. (A, B) Gascoyne River Middle Branch Bridge area, (C, D, E) Three Rivers Station access road (various locations), (F) Neds Creek Station, 67 km ESE from Great Northern Highway. Photos: B. Bush.

consistent ground colour and uniform, although more complex, body pattern of alternate transverse rows of small white spots and larger black spots. It is my experience that the consistent similarities between members of this cohort cause them to be the most difficult to assign to a population.

With such a conservative group there is little morphological evidence referred to by Melville *et al.* (2016) regarding their taxonomic rearrangement. They do include the following for elevating *C. graafi* to full species "reflecting its morphological difference, isolated distribution and genetic distinctiveness" and with *C. infans* it is based on both morphological and molecular evidence.

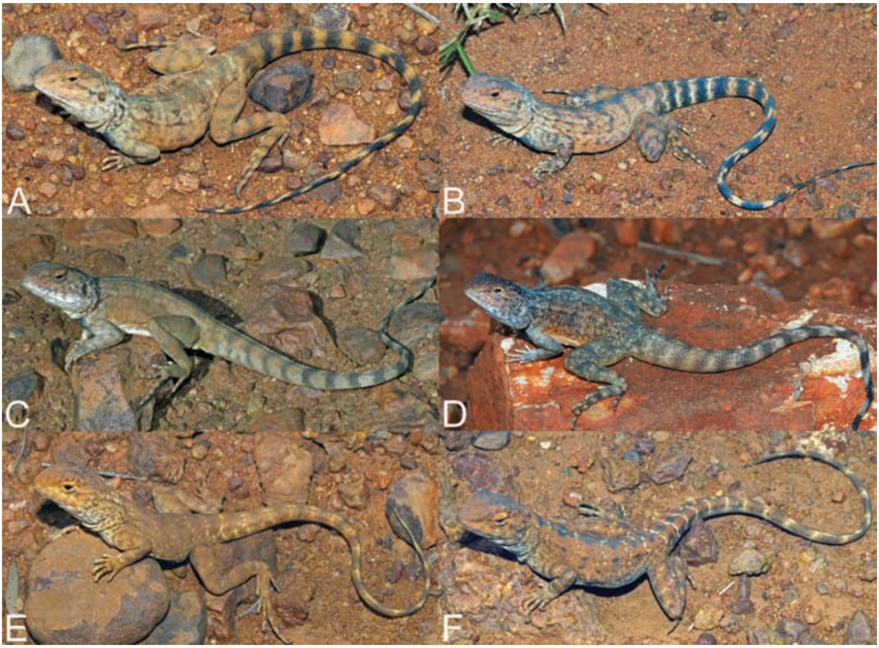

Figure 4. Variation in adult male ring-tailed rock dragons from the location of Storr's 1967 "*Ctenophorus mensarum* type series" in northern Murchison east of Meekatharra. (A), 89 km E, (B) 57 km E, (C) 45 km E, (D) 25 km S of Wiluna, (E) 57 km E, (F) 97 km E. Photos: B. Bush.

Methods

This study is based on field observations from the past 35 years when travelling in WA from the southern goldfields to the tropical Kimberley. During these trips, I visited both well-populated and remote areas to examine and photograph representatives of the local herpetofauna. I have documented 155 ring-tailed rock dragons from the Pilbara, Gascoyne and Murchison: 71 adult, 56 subadult and 28 juvenile individuals.

Visual observations of ring-tailed rock dragons and their behaviour were generally made opportunistically when camped in that respective area, or when purposely visiting particular sites to capture individuals of the local population to allow close examination. The primary technique employed to capture active lizards was noosing, although many individuals were found beneath rocks, cow pads, old vehicle parts and general rubbish or during warm months by head-torch at night when lizards are sleeping in open areas or sheltering beneath cover (Fig. 9).

Examination included measuring SVL and total length with a plastic ruler and noting the sex of subadults and adults. Photographs were taken of the throat, chest, femoral pores, precloacal pores and dorsum. The SVL

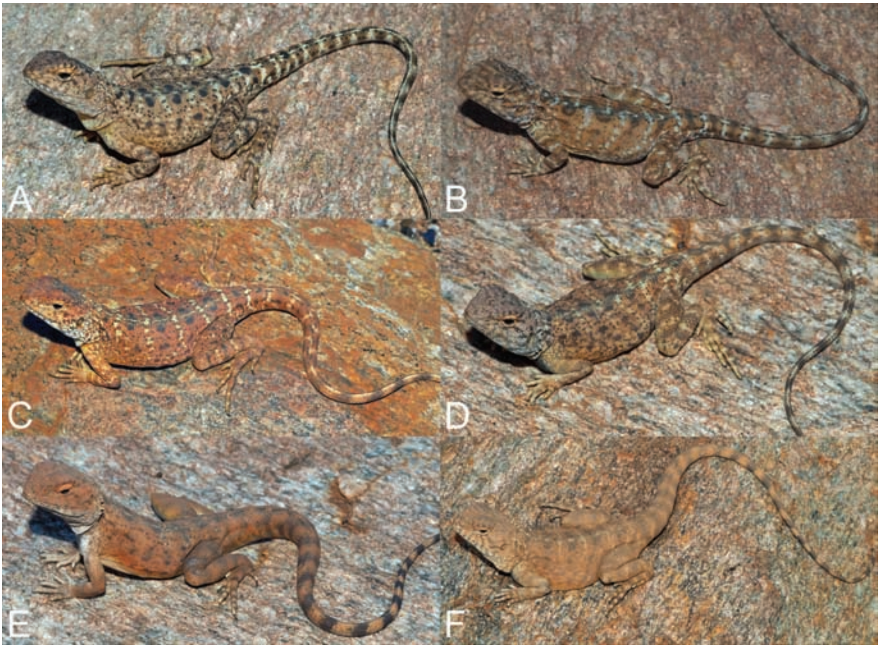

Figure 5. Variation in male southern *Ctenophorus caudicinctus* from the central Murchison. (A) 38 km S of Cue, (B) 45 km N of Mt Magnet, (C) 35 km S of Cue, (D) 38 km S of Cue, (E) 28 km S of Cue, (F) 27 km N of Mt Magnet. Photos: B. Bush.

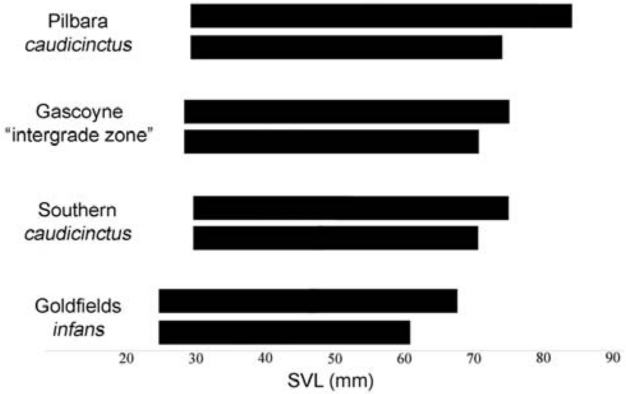

Figure 6. Comparative maximum adult ring-tailed rock dragon size recorded showing a north-south clinal reduction in size: males upper bar and females lower bar. Pilbara *Ctenophorus caudicinctus*, central southern Gascoyne (Storr's "*C. caudicinctus-mensarum* intergrade zone"), central Murchison (southern *C. caudicinctus*) and eastern Goldfields (*C. infans*).

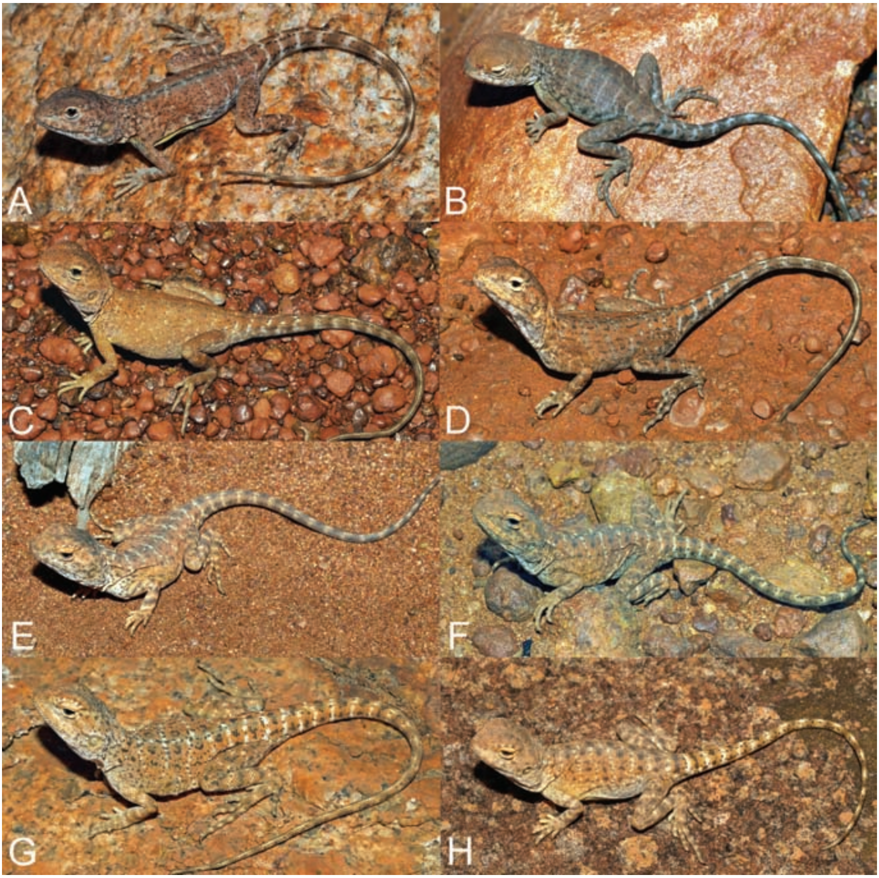

Figure 7. Comparison and variation in juvenile ring-tailed rock dragons. (A, B) Pilbara; (C, D) central southern Gascoyne "*Ctenophorus caudicinctus-mensarum* intergrade zone"; (E, F) northern Murchison (Storr's 1967 "*C. mensarum* type series" location) 45 km and 57 km E of Meekatharra; (G, H) central Murchison (southern *C. caudicinctus*) from near Cue. Photos: B. Bush.

sizes used here to assign individuals to their respective cohort are: ≤39 mm – juvenile (the size below which sex determination is difficult); 40–55 mm – subadult (the size that males commence the development of the chest patch); and ≥56 mm – adult (the size of smallest male southern *C. caudicinctus* with fully developed chest patch; see Fig. 10).

Some aspects of behaviour were also documented by photo and/or video. Video was especially required to document complex head-bobbing sequences that can only be adequately analysed after filming and replaying in slow motion.

All images, montages and photos used here are the work of the author.

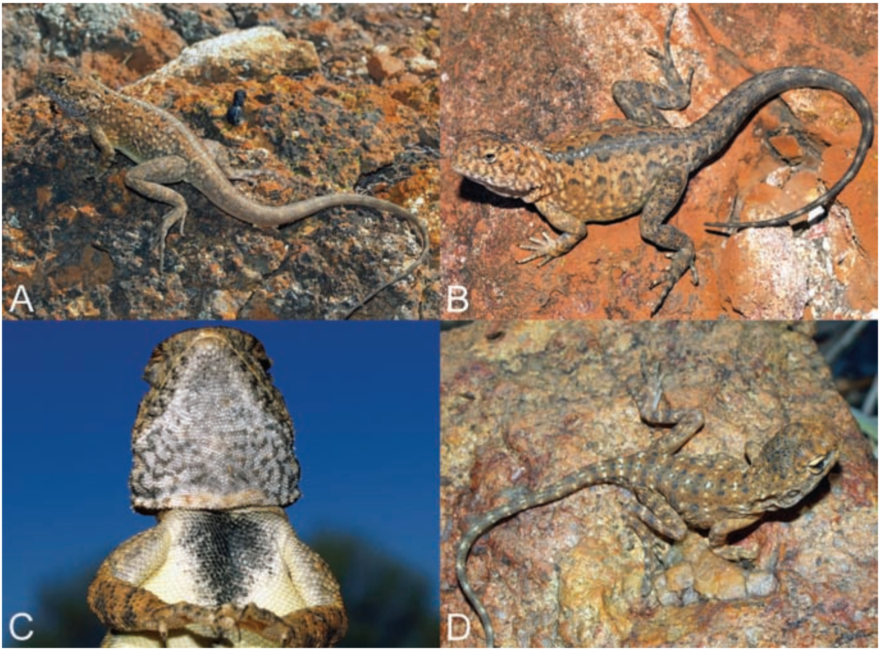

Figure 8. *Ctenophorus infans* is the most southerly occurring ring-tailed rock dragon in WA. (A) adult male, (B) adult female, (C) chest patch of the adult male illustrated here (D) juvenile. Photos: B. Bush.

Field observations and discussion

Behaviour

Basking

Ring-tailed dragons are predominately diurnal sun-loving lizards with recorded body temperatures when active of between 36.5°C and 39°C (Licht *et al*. 1966; Bradshaw & Main 1968). They are frequently observed in the warmer months basking on slightly elevated sites such as small sticks or stones with their dorsum to the sun. As the temperatures rise the basking becomes more intermittent and for shorter periods, with extended periods of foraging on the ground. Foraging involves running short distances, stopping and feeding on several ants in the immediate area before running to another position and repeating the process. Opportunistically much larger arthropod prey (cockroaches, grasshoppers, spiders, etc.) that move into view are also pursued and consumed.

As the temperature rises even further and the ground becomes quite hot (e.g. >50°C), stationary individuals raise the toes on their hind feet so that only the heels contact the ground (Fig. 11; see also Melville & Wilson 2019: p 42). They may also do this with the forefeet but not as frequently. By the early afternoon, they progressively move to more elevated vertical sites

Figure 9. Ring-tailed rock dragons found torpid during cool weather beneath anything laying on the ground, especially dry cow pads, flat rocks and rubbish (adult upper and juvenile lower). Photos: B. Bush.

Figure 10. Fully developed chest patch in small adult male southern *Ctenophorus caudicinctus* of SVL 57 mm from 38 km S of Cue. Photos: B. Bush.

Figure 11. Pilbara *Ctenophorus caudicinctus* male displaying to competitors and females from an elevated position in the Chichester Range, 80 km S of Karratha. Photos: B. Bush.

off the ground to avoid the increasing temperature, particularly the radiated heat rising off the ground as well as the direct rays of the sun, by perching in the shade of large boulders, which they regularly climb as basking sites, termite mounds or tree trunks (Fig. 12). Juveniles are usually on the stone-strewn ground in areas densely vegetated with grasses, especially *Triodia* and are rarely seen off the ground. The subadults and adult females also avoid the more elevated areas and are most abundant around the periphery of the larger outcrops amongst low boulders, they readily climb these as basking sites. These places are also where the grasses are quite dense and overgrowing the boulders, providing the lizards a quick retreat within for protection from predators or when disturbed. The subadults and adults will also make excursions into open areas between isolated tussocks of grass and rely on their speed to escape threats by retreating into the safety of the grass. Although juveniles will occasionally enter open areas also, they tend to defensively freeze with head and body in contact with the ground as if relying on camouflage to avoid predators much in the same way as pebble-mimic dragons (*Tympanocryptis* spp.).

Head bobbing

Towards the end of winter on the Pilbara coast and a little later (early spring) inland adult males are often observed occupying the highest places well above the immediate surroundings. Here they interact with other males similarly positioned and females within their vision by combining a series of one or two controlled head bobs. The head bobbing is followed by a slow

Figure 12. In summer ring-tailed rock dragons perch off the ground during the hottest part of the day on the shaded side of large boulders, termite mounds, tree branches, trunks of trees, etc. Left: gravid females, right: adult males. Photos: B. Bush.

deliberate partial straightening of the forelimbs pushing the forebody upwards and displaying the black chest patch to both competitors and potential mates (Fig. 11).

The above is just one of several head bob sequences observed within a population and performed by all members including juveniles and subadults. It is usually but not always performed after a short run with the least complex being a single head bob with the whole movement not rushed and in even time. It commences in the alert heads-up position, then following a slight elevation in the head position it is lowered before being raised and returned to the alert position, although through this whole action the head is always held angled upward from the ground and does not include any bending of the neck or nodding, rather it is facilitated by keeping the head stationary and raising and lowering the shoulders with a slight straightening and bending of the forelimbs. This may be a single stand-alone sequence, or it may be followed quickly by the same sequence a second time extending the series, although to the naked eye it looks like two rapid head bobs. The most complex and common head bobbing pattern/sequence performed by subadults (although to the naked eye at standard speed appears to be a single head bob followed immediately by a forebody shiver), however, when slowed down it is a single head bob at the same speed as described above, followed by a series of two or sometimes three extremely rapid head bobs.

Starting from the alert heads-up position, all four simplified sequences begin the same way with a single clear up-down-up (#1 below) and then may be extended as follows.

1. *Up, down, up* at an even time.
2. *Up, down, up…. up, down, up* both series at an even time.
3. *Up, down, up* at even time followed by very rapid *down, up, down, up.*
4. *Up, down, up* at even time followed by very rapid *down, up, down, up, down, up* with the final bob diminishing to marginally more than a shake of the forebody.

Although body re-positioning and limb waving have been observed in *C. slateri* (Ramos & Peters 2017) in the western MacDonnell National Park, they state that this pattern is not present during territorial displays. I have not observed this pattern in Kimberley *C. slateri*, nor in any population of *C. caudicinctus* or *C. infans*.

Nocturnal basking and winter brumation

Individuals, particularly adults, are commonly encountered sleeping at night in exposed places lying flat with eyes closed, head on the ground and body against the warm substrate assumedly to absorb the residual heat. This occurs in many diurnal lizards during summer and especially in the gravid females (pers. obs.). In this latter group, it is believed to facilitate the more rapid development of oviducal eggs by raising body temperature above the cooler ambient. However, this is not the only purpose because the behaviour occurs in both subadults and males, albeit less frequently, the accelerated digestion of food and extending the growth period may be contributing factors to this opportunistic thermoregulation. Nocturnal basking does contribute to lizards being struck by cars at night, especially in the Pilbara where rocky habitats are often dissected by roads. The prevalence of this nocturnal thermoregulatory behaviour is less frequently observed in the south. Bush *et al*. (2007) report briefly on similar behaviour associated with reproduction in tail-squirting geckos (*Strophurus* spp.).

This exposed nocturnal sleeping has also made the lizards an easy target for predators to opportunistically locate individuals. Although snakes can encounter sleeping lizards while foraging, the two species with a predisposition for hunting sleeping dragons are *Suta fasciata* and *S. punctata* (Shine 1983; Bush 2017).

During the winter months, *C. caudicinctus* can be found torpid or brumating (reptile equivalent to mammal hibernation) under objects laying on the ground, particularly easy-to-lift flat rocks and dry cow pads. I suspect the benefit of the latter would be their insulation properties limiting the loss of ground temperature overnight, especially inland where much of its range experiences zero air temperatures at this time of the year. In the southern parts of the range in late autumn, dragons excavate chambers or short burrows in the soil beneath rocks. These may be on low outcrops but more often they are dug around the outcrop's periphery likely owing to the softer soil there.

Comparison of habitat preferences of C. ornatus *and* C. caudicinctus

In areas where both *C. ornatus* and southern *C. caudicinctus* are found, their alternative ecologies and especially habitat preferences separate them quite dramatically. Although both occupy rocky places, *C. ornatus* is a dorsoventrally flattened species that is observed on the large open expanses of granite and uses horizontal crevices as a primary refuge. In contrast, *C. caudicinctus* occurs among the smaller boulders in the stone-strewn intervening areas and when disturbed, seeks refuge among vegetation and in small horizontal or vertical crevices. Figure 13 shows an aggregation of eight *C. ornatus* found torpid on an outcrop beneath an exfoliated rock forming a horizontal crevice in August 2015.

Sexual dimorphism

Storr (1967) reported that males attain a larger maximum SVL than females in all his designated subspecies (males/females, in mm: Pilbara *C. caudicinctus* 89/74; *C. mensarum* = southern *C. caudicinctus* 81/62; *C. infans* 67/60). In his description of the largest subspecies *C. c. macropus* (now *C. slateri*) on page 53, he states the holotype, SAMA R3229 in the South Australian Museum (SAMA) is 89 mm and that the paratype, USNM 128751 in United States National Museum (USNM, Smithsonian Institute) is larger at 101

Figure 13. Aggregation of eight *Ctenophorus ornatus* torpid near Wubin, WA in August 2015. Photos: B. Bush.

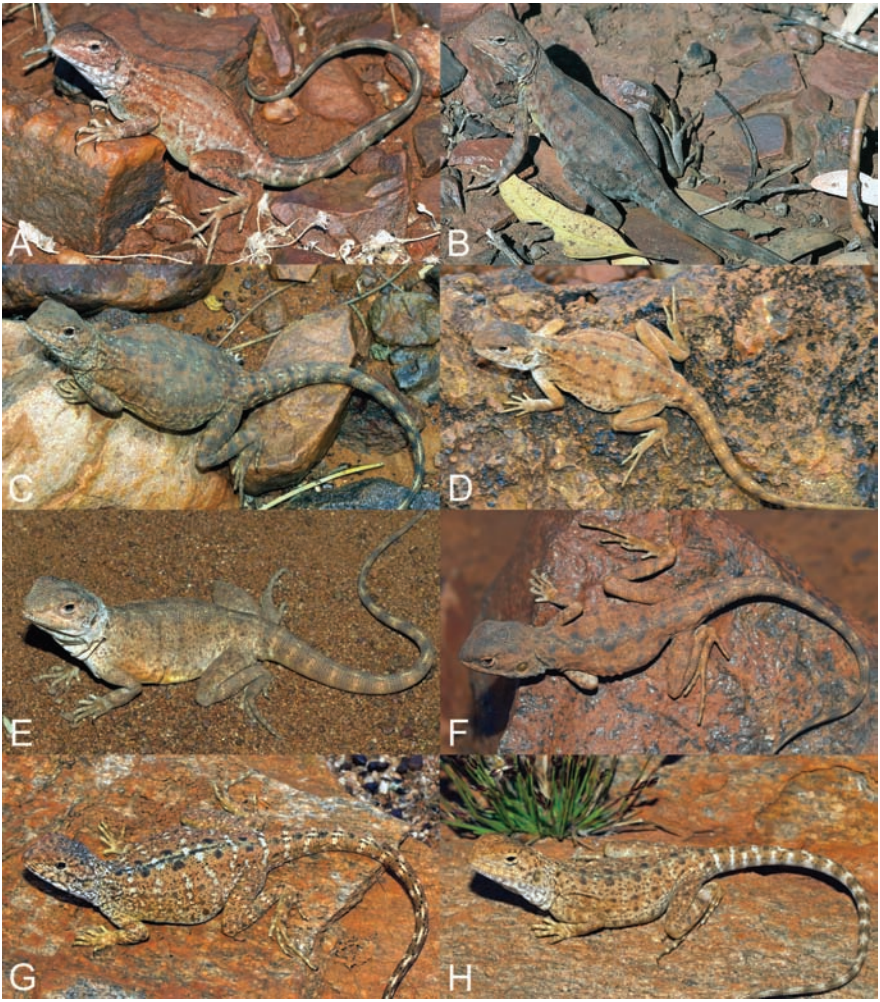

Figure 14. Comparison and variation in adult female ring-tailed rock dragons. (A, B) Pilbara *Ctenophorus caudicinctus*; (C, D) central southern Gascoyne "*C. caudicinctus-mensarum* intergrade zone"; (E, F) northern Murchison ("*C. mensarum* type series" location); (G, H) central Murchison (southern *C. caudicinctus*). Photos: B. Bush.

mm with both being collected on 30 September 1948 near Oenpelli, NT. Apart from this brief mention, Storr does not refer to this large individual again, and I have been unable to find any further reference to it elsewhere.

I also observed sexual size dimorphism, although the largest male *C. caudicinctus* I measured in the field was smaller than Storr's (81 vs. 89) and my largest southern female exceeded his (70 vs. 62). Maximum SVLs (mm) for *C. caudicinctus* presented in the literature vary and in some of these cases they may have been rounded up, e.g.: 89 (Storr *et al.* 1983); 89 (Greer 1989); 100 (Ehmann 1992); 100 (Bush *et al.* 2007); 100 (Cogger 2014); 90 (Melville & Wilson 2019); and 81 (present study). For a comparison of the regional size and sexual size dimorphism recorded see Figure 6.

As with many Australian agamids (Wilson & Knowles 1988: p. 28; Greer 1989: p. 9; Melville & Wilson 2019: p. 21; pers. obs.), *C. caudicinctus* exhibits some variation in colour and pattern that is evident across all members of any given population, being most pronounced in adult males and to a lesser degree in juveniles, subadults and adult females (Figs. 2–5, 7 & 14). The colour and pattern intensity may also be influenced by an individual lizard's mood, body temperature and season.

Sex can be readily determined in adults and subadults but not in juveniles ≤40 mm. It is from this size that the black chest patch is seen in adult males but absent in females (Figs. 15A vs. 15B) begins to develop as indicated by a darkening of the chest in subadult males. The progressive development of the patch relative to size is shown in Figure 16 (middle column). The chest patch may temporarily lose intensity or entirely vanish in males found at night during the warmer months sleeping under cover or when brumating during winter but returns quickly when the individual is disturbed or when it becomes active.

Interscalar femoral and precloacal pores occur in juvenile, immature and adult members of both sexes, but contribute little to identifying the sex of an individual. Even though there are marginally more pores in males than females: 30.6 (24–40; N 35) versus 27 (20–36; N 24), the substantial overlap in numbers between the sexes renders the counts of little relevance for sexing individuals. In older adult males, which already have the black chest developing, these pores become far more active than in juveniles, subadults and females, with this activity increasing their comparative diameter. The secretions can be long conical protrusions and therefore also dimorphic, but usually only in larger males. Figure 15E shows these secretions and allows a comparison of the pores in an adult male (SVL 72 mm) and gravid female (SVL 67 mm) found on the same day in January 2017 near Middle Branch Bridge, Gascoyne River (25°11'02"S, 119°19'46"E) under an old car door.

When examining the base of the tail immediately following the cloaca in Figure 15C and all individuals illustrated in Figure 16 (right column) there is an external indication of male hemipenes in the form of a swelling to either side of the midline that extends laterally and is deeply indented posteriorly at its centre by a depression. Note that this is absent in the sexually mature female illustrated in Figure 15D with the posterior margin being straight. However, it is not always as obvious, so I am hesitant to place too much reliance on it in determining the sex of small or poorly marked individuals in the field.

The size of the upper and lower canine teeth may be another sexually dimorphic indicator in adults as shown in Figure 17. Those in a male of SVL 76 mm photographed in November are much larger than in a comparable-sized gravid female of SVL 74 mm photographed in mid-March. The

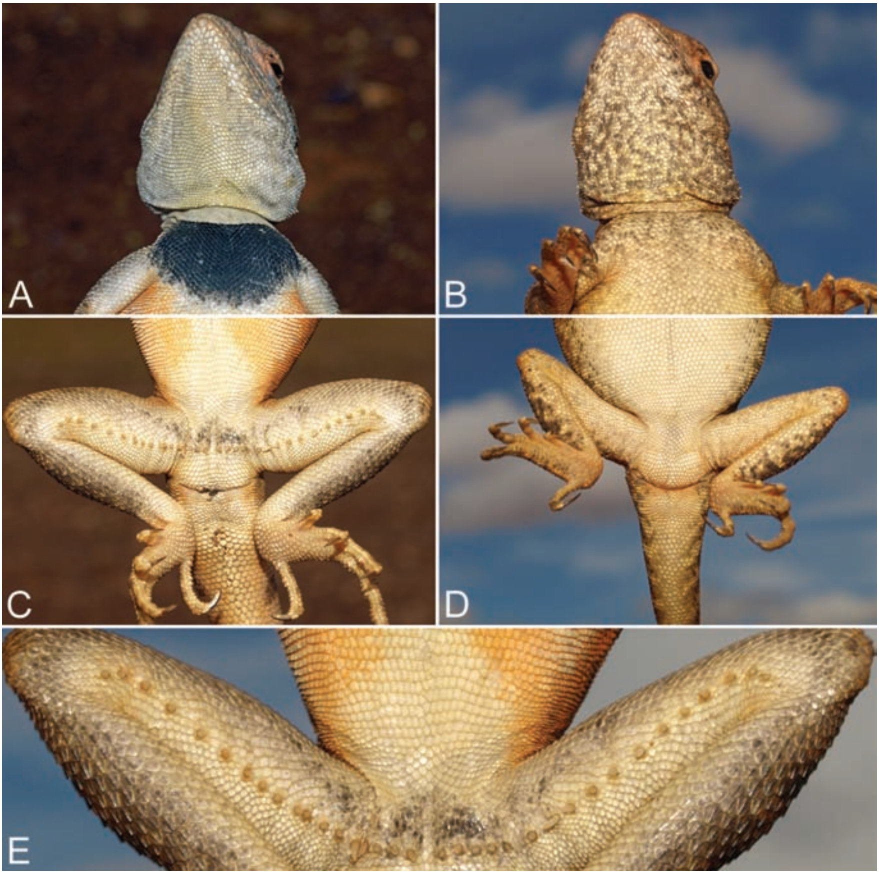

Figure 15. Ring-tailed rock dragons from central southern Gascoyne showing the obvious sexual dimorphism in colour and development of precloacal and femoral pores. (A,C) male; (B, D) female; (E) a close up of the conical protrusions from active pores in male. Photos: B. Bush.

growth of the canines in adult males may be seasonal preceding reproductive behaviour and assist the males in restraining females during mating.

Geographical colour and pattern variation in adult males

Colour is significant in determining polymorphic and monomorphic agamid lizard lineages (Dong *et al.* 2021) and is used to differentiate species in the saxicoline *C. decresii* group (Houston 1974; Gibbons & Lillywhite 1981). The importance of male colouration in species diagnosis in that group has become even clearer (Johnston 1992; McLean *et al*. 2013) as has camouflage and interactions between individual lizards (McLean

Figure 16. Male ring-tailed rock dragons showing the progressive development of black chest patch relative to size (SVL mm) and the lack of this development in the femoral and precloacal pores until they become active in older males. (A 42, B 47, C 54, D 60, E 68, F 81). Photos: B. Bush.

et al. 2014, 2015). In contrast, male *C. caudicinctus* show both inter and intrapopulation variation. A sample of Pilbara adult male *C. caudicinctus* is illustrated in Figure 2. Here, the ground colour is variable, and this is especially so in Figure 2E from near Munjina where the ground colour is darker in this part of the Hamersley Range. This is also seen in individuals of the local military dragon (*C. isolepis*; unpublished data). However, there are three constant characteristics that the Pilbara ring-tailed rock dragons tend to share: they all possess a black chest patch, black bands along the length of the tail and two wavy dark brown longitudinal lines on the flanks.

Moving south into the central southern Gascoyne (Storr's 1967 intergrade zone), the black chest patch and the two wavy dark longitudinal lateral lines are still consistent characters retained in adult males, but the black tail bands (consistent in Pilbara *C. caudicinctus*) become less defined (Fig. 3). Of the six male individuals illustrated, only A and B retain these, while in C and D they have significantly faded and in D are starting to fragment, while in E and F only remnants remain. Illustrated in Figure 4 from further south in the northern Murchison where Storr's "*C. mensarum* type series" originated, there is a similar reduction of the tail bands and in the consistency of the two wavy lateral lines, with these absent in E and F.

Storr (1967) referred to intergrading between typical (nominate) *C. caudicinctus* and "*C. mensarum*" and commented that if a boundary can be defined between them, it would probably be found along the Ashburton River, upper Gascoyne and Ilgararri Creek drainages (see Fig. 1). The central southern Gascoyne population, as

Figure 17. Larger canine teeth in a male ring-tailed rock dragon (SVL 76 mm), 38k N of Munjina (left photo), compared with that of a gravid female (SVL 74 mm), near Tom Price (right photo). Photos: B. Bush.

Figure 18. Variation in southern *Ctenophorus caudicinctus* from one rock outcrop 40 km N Mount Magnet. Photo: B. Bush.

presented in Figure 3 are all recorded along or just to the south of the east-west midline of Storr's hypothetical boundary which he suggested might be between latitudes 24° and 26°S. I have found the transition from Pilbara *C. caudicinctus* to southern *C. caudicinctus*, hence the intergrade zone, to be generally the same as Storr's interpretation with adult males along latitude 25°S visually the most different to both the Pilbara and the northern Murchison "*C. mensarum* type series" populations. In 1967, Storr had little material to work with apart from juveniles and subadults, so the southern boundary (along latitude 26°S) of this intergrade zone may also have comprised some of his "*C. mensarum*" at the time. However, south of both this east-west zone and the northern Murchison "*C. mensarum* type series" band, the morphological changes are more pronounced, with a complete loss of the black anterior tail bands being replaced with marginally darker bands in some, but in most these are reduced to dark spots over areas of ground colour between narrow white bands and a merging in body colour and pattern between males (Fig. 5) and females (Figs. 14G & H). This has resulted in the sexual colour dimorphism dorsally obvious further north to be almost non-existent in the southern *C. caudicinctus* population where it is morphologically intermediate between

Pilbara *C. caudicinctus* and *C. infans*. Compare *C. caudicinctus* males in Figure 2 and females in Figures 14A & B with southern *C. caudicinctus* males (Fig. 5), females (Figs. 14G & H) and assorted individuals from the one location in Figure 18. Also, the central southern Gascoyne and northern Murchison (type series) form is observed equally abundant on sparse stone-strewn heavy loam substrates (Fig. 19C) and on stony hills (Fig. 19D), although southern *C. caudicinctus* appear far more habitat-specific being almost wholly restricted to large, low granite outcrops (Figs. 19E & F) and *C. infans* to more elevated rocky outcrops (Figs. 19G & H).

Seasonal fluctuation in population demographics and longevity

The seasonal demographics follow the usual pattern (Shine 1989; Bush 1992; Melville & Wilson 2019: p 47) seen in the southern hemisphere in many oviparous reptiles that lay multiple clutches during a breeding season (Fig. 20). That is, early spring mating, late spring and early summer egg deposition, late summer and early autumn hatching with juveniles abundant throughout autumn, peaking in the late part of that season (May) and declining through winter. Subadults are abundant in late autumn through early winter and peak again in late spring becoming adults at this time, and adults occur throughout the year. The extended period of occurrence observed here in juveniles and subadults is probably a result of both the extension of the breeding season caused by multiple-clutching and the additional influence of the graduated temperature over the study area (where on the coast minimum temperatures are higher than inland areas where extremely low autumn and winter temperatures can often be <0°C). Exposure to these low temperatures would retard lizard growth and therefore extend the seasonal occurrence of these two cohorts within the wider population.

In the Pilbara south of Karratha through the Gascoyne to north of the Ashburton River, adult females were recorded with well-developed palpable eggs in December (2), January (5), February (8) and March (11). These heavily gravid individuals were most often found inactive at night with their ventral surfaces pressed against the warm substrate. The SVL in this gravid series was 61–70 mm. Clutch sizes of 4–8 have been recorded (Bradshaw 1981; Pianka 1986; present study).

Based on examination of specimens, Storr (1967) suggested Pilbara *C. caudicinctus* might be short-lived, breeding at about nine months of age and dying a few months later. Juveniles hatching between March and June and acquiring adult characteristics when about 55 mm SVL (commencing at 40 mm in males; present study) between June and September (but as late as November; present study) and dying after 12 months. Storr categorised individuals as adults when SVL in males was 76–89 mm, females 57–74 mm; as subadults in males 56–73 mm, females >58 mm and as juveniles (unsexed) 23–55 mm. During this study, the size ranges of the three arbitrary age classifications are adult >59 mm, subadult 40–59 mm and juvenile <40 mm. Adult males and females were found throughout the year, so I suspect there is an overlap with late-maturing adults and maybe other mature individuals living for two years or longer.

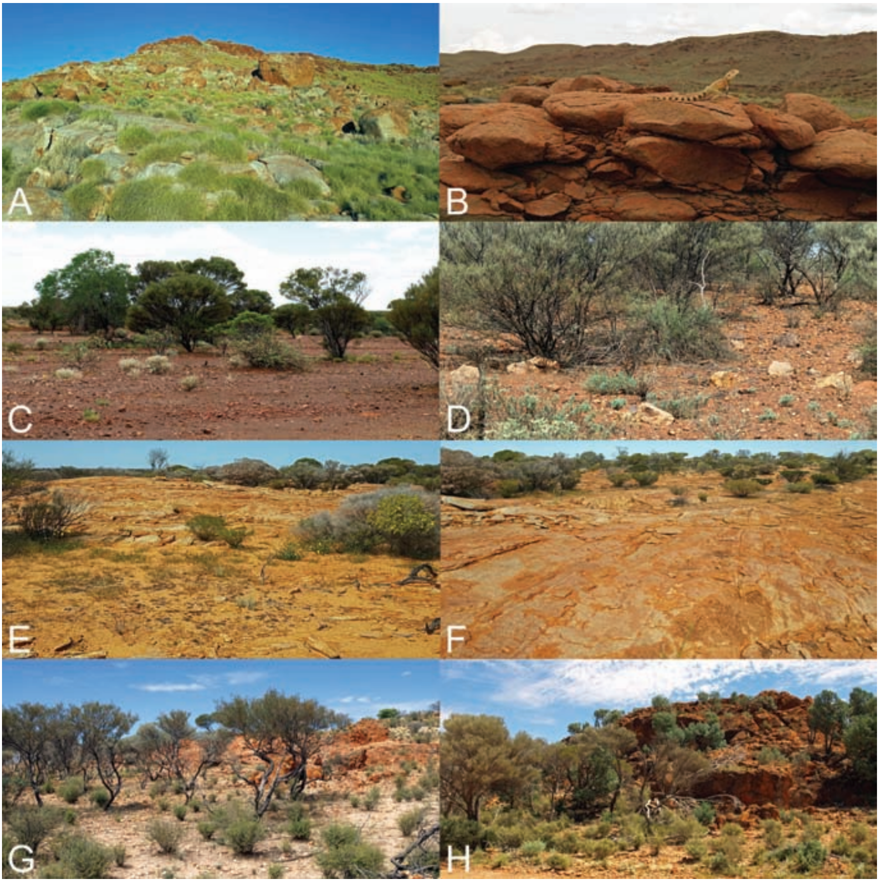

Figure 19. A range of habitats that ring-tailed rock dragons occur in from rocky outcrops and stone-strewn flats to gravelly and clay substrates with only sparsely strewn stones. (A, B) Pilbara (*Ctenophorus caudicinctus*); (C, D) central southern Gascoyne and northern Murchison respectively ("*caudicinctus-mensarum* intergrade zone" and "*mensarum* type series"); (E, F) central Murchison (southern *C. caudicinctus*); (G, H) WA Goldfields, east of Laverton (*C. infans*). (A) Spinifex and stony hill east of Port Hedland, (B) layered granite hills, Chichester Range, (C) stone-strewn flat that is typical of much of the habitat in the Gascoyne, Middle Branch Bridge, Gascoyne River, (D) low stone-strewn hill west of Wiluna, (E) low granite outcrop near Cue, (F) granite flat near Mount Magnet, (G) rocky outcrop east of Laverton, (H) rocky outcrop east of Laverton. Photos: B. Bush.

Observations of captive-bred *C. infans* suggest that under optimum conditions it can live into its sixth year and produce multiple clutches (2–5 in a season) of 5–7 eggs as recorded by Australian dragon specialist keeper, Mark Hawker of Narooma, NSW (pers. comm.; July 2021) he said that he got his first group comprising six hatchlings in

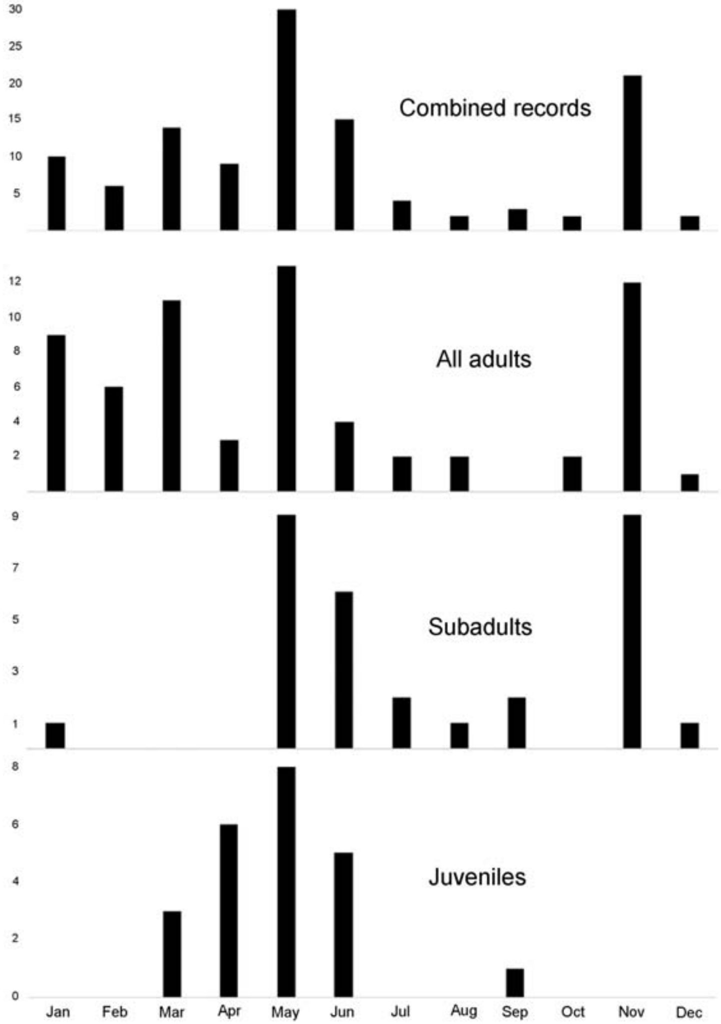

Figure 20. Monthly frequency of ring-tailed rock dragons in all cohorts examined during this study.

April 2016 and captive individuals were still breeding after two years of age under good conditions. At the time of our correspondence, he had individuals that were four years old that produced two clutches of eggs in the most recent summer and one male individual (the last surviving from the original six acquired in April 2016) that was at the time showing signs of age-related physical deterioration (preceding death) in the early part of its sixth year. However, he relayed that in his experience *C. infans* appears to be the most robust of the ring-tailed rock dragons he has kept in captivity to date, which have included *C. ornatus* and *C. slateri*.

In July, *C. caudicinctus* in the coastal and near-coastal Pilbara are active from the mid-morning until the late afternoon when daytime temperatures have risen to 23°C and continue rising to about 30°C for most of the day, but inland at a site 70 km north of Newman there is similarly no activity in the morning when temperatures are below 22°C until early afternoon and then only minimal activity as the temperature rises to a maximum marginally exceeding 23°C. The higher Pilbara coastal and near coastal temperatures may result in extended activity periods both during the day and for much more of the year, and this would possibly shorten longevity compared with the inland and southern populations, which spend much more time brumating with this contributing to a greater longevity.

Fluctuations in seasonal conditions in the wild would probably influence longevity, especially the sudden and dramatic impact of fires and floods and the reduction in food that may be the immediate aftermath of these events. I hypothesise a life span of two to four years would be typical in all members of the *C. caudicinctus* group.

Anomalous specimens

The southerly distribution of ring-tailed rock dragons in the eastern Murchison is generally well to the north and east of the mulga-eucalypt line, with museum records suggesting the southern boundary is 35 km northeast of Menzies in the central northeastern goldfields (*C. infans*) and northwest of Leonora (*C. caudicinctus*), then just to the northwest of Lake Noondie near Yuinmery Station homestead, Mount Magnet, west to Tardie and Mileura Stations in the Midwest region; and east to Mt Fisher on Yelma Station in the Wiluna Shire. However, there are three records from much further south, deep into the eucalypt-dominated Western Woodlands and Perth metropolitan areas identified as *C. caudicinctus* that are best-considered anomalies and ignored with respect to the group's WA distribution until further specimens are identified from these respective locations. The specimens are NMV R887 with little associated data attached but supposedly collected in South Perth and held in Museums Victoria, Melbourne; AM R3081 from Boulder collected by W. Campbell in December 1900 and held in Australian Museum, Sydney; and WAM R126476 from near Lake Cowan, 7 km southeast of Higginsville collected by Biota in January 1996 and held in the Western Australian Museum. This is 293 km south of the most southerly location previously known for ring-tailed rock dragons and 230 km south of the mulga-eucalypt line. The inadvertent transport and possible introduction of reptiles from the mulga belt north of Goongarrie to the mallee-dominated Esperance sandplain has been previously documented by Bush (1987).

In southern WA, disregarding the poorly documented Perth record, where both inland anomalous specimens were found, it has been prospected and mined since 1893 with much movement of both people and their personal and commercial equipment throughout these regions. Both isolated records may

Figure 21. Ring-tailed rock dragon (WAM R126476) - SVL of 57 mm, collected on 14 January 1996 from 7 km southeast of Higginsville in 31°50'S 121°43'E and believed by the author to be a southern *Ctenophorus caudicinctus* inadvertently introduced from possibly the Mt Magnet area. Photo: B. Bush.

not represent naturally occurring populations, but rather individual records of inadvertently transported dragons introduced to these places from north of the mulga-eucalypt line.

A comparison of adult *C. infans* (Figs. 8A & B) with the Higginsville specimen (Fig. 21) indicates that it is not *C. infans*. When compared with the southern *C. caudicinctus* individuals depicted in Figure 18, it is almost identical and adds support to the argument that the Higginsville individual was inadvertently introduced. In addition, *C. infans* is the most southerly species of the group, thus potentially forming a barrier excluding *C. caudicinctus* from naturally dispersing south to the Higginsville area.

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