

Anti-predation behaviour of Dickerson's collared lizard, *Crotaphytus dickersonae*

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Abstract—Males of Dickerson's collared lizard (*Crotaphytus dickersonae*) are conspicuously bright blue in colour and can be detected at great distances. In contrast, females are brown and much less conspicuous. Given the visibility of males to predators, the question arises how they avoid predation and whether the sexes differ in anti-predator behaviour. Using a slowly approaching human as a simulated predator, approach and flight distances were recorded, as were the presence of other anti-predation responses such as pursuit deterrence signalling, distraction behaviour and aggressive threat. The lizards were captured and physical data such as cloacal temperatures, weight and snout-vent length were obtained. To assess further the effect of coloration on predation pressure, test subjects were painted to make them inconspicuous (brown) or conspicuous (blue) and recaptured after a week. After shedding their painted skin, subjects were approached one final time. Few direct relationships were found between anti-predation displays and body weight, size or temperature. Exhibition of pursuit deterrence signalling or distraction behaviour was rare, and no subject displayed aggressive behaviour (except when caught). Interestingly, males fled sooner, and tended to use more refuge than females, which probably indicates stronger predation pressure on males. However, an overall low use of refuge, the observer's ability to approach most subjects closely before they fled, and few sightings of potential predators, suggest that weak local predation pressure helps to explain why sexually selected conspicuous male coloration has been able to evolve in *C. dickersonae*.

Keywords: anti-predation behaviour; approach distance; conspicuous; *Crotaphytus dickersonae*; refuge; predation pressure.

INTRODUCTION

In nature, organisms are subjected to selection pressures that result in differential survivorship and reproductive success. One such selection pressure is predation,

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and individuals that successfully avoid predators have the potential to contribute more offspring to the next generation. Excluding the special case of warning coloration, predator avoidance is best facilitated by strategies which result in going undetected by predators. Yet, sexual selection often favours conspicuous coloration through intra-sexual competition and mate choice (Anderson, 1994). Conspicuous coloration makes prey more visible to predators, however. The coloration of males and females in a given species/population will thus reflect the sum of different selective pressures on each sex at the local geographic scale (Endler, 1992).

It has been argued that conspicuous coloration in collared lizards signals resource holding potential (Baird et al., 1997), but, with a few exceptions, both sexes in most collared lizard species are relatively inconspicuous in coloration. Dickerson's collared lizard, *Crotaphytus dickersonae*, is one of those exceptions. In this species, sexually mature males exhibit bright blue body coloration (McGuire, 1996). By comparison, females are a dull brown colour, similar to that of local soil and rocks. Like all collared lizard species female *C. dickersonae* display bright orange bars and blotches on their sides when gravid, which stimulates male courtship (Ferguson, 1976; Baird, 2004). Given the visibility of these lizards, how do they manage to avoid predation?

Conspicuous lizards may compensate for increased predation pressure with anti-predation behaviour (Lima and Dill, 1990; Forsman and Appelqvist, 1998; Martin and Lopez, 1999a), and several anti-predation behaviours have been described for lizards:

- i) *Scanning behaviour*: Scanning the surroundings frequently increases the odds of detecting a predator, and thus facilitates an escape. Scanning rate is anticipated to co-vary with predation pressure. For example, scanning rates in birds are lower in the absence of predators (Fernández-Juricic et al., 2004). Likewise, females of the sun skink (*Lampropholis delicata*) live in groups, diluting the chance of capture, and the time spent vigilant decreases with increasing group size (Downes and Hoefler, 2004).
- ii) *Pursuit deterrence signalling*: Many predators rely on surprise to capture their prey. In some species, a prey animal that detects a predator may signal to the predator that it has been seen (Woodland et al., 1980; Hasson, 1989). Having lost the advantage of surprise, many predators will abort the hunt when detected (Hasson, 1991). The benefit of signalling to the predator is obvious for the prey in this case, but the predator also benefits by moving on and searching for less wary prey. The pursuit deterrence hypothesis predicts that signalling should be performed towards the predator (Hasson, 1991), and that the prey should signal while stationary (Leal and Rodríguez-Robles, 1997).
- iii) *Imposing and aggression*: Prey can attempt to intimidate a predator by making themselves appear larger than they actually are (Pianka and Vitt, 2003). Prey can also threaten the predator with aggression, by gaping and threatening to bite (Cuadrado et al., 2001) or by actually biting (Burnett et al., 1985). When a

predator does not retreat, however, the only option remaining is to flee. Several behaviours associated with fleeing can be measured, as follows:

- iv) *Approach distance*, also called flight initiation distance (Blumstein, 2006), is the distance the prey allows the predator to approach before fleeing. This distance is crucial, because hunting success depends on close approach for many terrestrial predators (Murray et al., 1995). Many prey species flee to refuge (Greene, 1988), and approach distance has been found to depend on the distance to refuge or degree of cover available (Bulova, 1994; Martín and López, 1995; Cooper, 1997, 2003; Cuadrado et al., 2001).
- v) *Flight distance*: The distance a lizard flees depends on distance to cover (Bulova, 1994), although it may be affected by other factors as well. In the greater earless lizard, *Cophosaurus texanus*, flight distance was positively correlated with approach distance; an individual that fled earlier also fled further, suggesting that level of wariness influenced both approach and flight distance (Bulova, 1994).
- vi) *Distraction behaviour*: The prey can attempt to confuse the predator by moving in an erratic manner; the prey's escape vector is made unpredictable by rapidly changing the direction of movement. Such behaviour should be displayed immediately before or during flight (Leal and Rodríguez-Robles, 1997). Species in which distraction behaviour occurs are usually cryptically coloured as this facilitates escape once they have stopped fleeing (Hasson et al., 1989).
- vii) *Refuge use*: Lizards often react to predators by fleeing to a refuge (Blázquez et al., 1997; Cooper, 1997, 2003), and the presence of a predator has been shown to increase refuge use (Martín and López, 1999a). Increased predation pressure stemming from conspicuous coloration should therefore increase refuge use.

In this study, anti-predation behaviours of the conspicuously coloured *C. dickersonae* males were compared to those of the less conspicuous females, using human approach as a simulated predator attack. In addition, experimental subjects were painted to be inconspicuous (brown) or conspicuous (bright blue), and were released to test whether changes in visibility to predators would influence anti-predation behaviour. After shedding their painted skin, subjects were approached a final time to determine if they had adjusted their anti-predation behaviour in response to anticipated changes in predator approach frequencies. Sightings of potential collared lizard predators in the study area also were recorded as an ecological estimate of predation pressure.

MATERIALS AND METHODS

Study subjects: The distribution of Dickerson's collared lizard (*Crotaphytus dickersonae*) is restricted to rocky mountainous habitat on Isla Tiburon in the Sea of Cortez and the adjacent mainland in western Sonora, Mexico (McGuire, 1996).

The study took place in the coastal hills near the village Bahía de Kino, during the lizards' morning activity period from May through August 2005. Both sexes in collared lizards are highly territorial (Husak and Fox, 2003) and establish their territories early in the active season, which for *C. dickersonae* begins in mid-March (McGuire, 1996). By the time this study commenced, all territories were presumed to be established with little or no dispersal by territory-holding adults.

Experiment: When a subject was detected at a distance large enough for the observer not to influence the subject's behaviour (>10 m), the number of times the lizard exhibited scanning behaviour (turning the head to look to one side or looking upwards) was counted over a 5-min period. Although it was not possible to distinguish between scanning for predators and scanning for prey or conspecifics, it is considered that the subjects should scan often when predation pressure is high.

The subject then was approached by a human acting as a surrogate predator (Martín and López, 1999a; Cooper, 2003), at a slow pace that decreased in speed with increasing proximity to the subject. During the approach all occurrences of potential pursuit deterrence signals were recorded.

Approach continued until the subject fled; the behaviour of the lizard during flight was scrutinised for distraction behaviour. Approach distance was measured (distance of observer to subject at the moment the subject fled), as was the flight distance (how far the subject fled) to the nearest 0.05 m. If the lizard fled into refuge, the distance from its pre-fleeing location to the refuge was determined.

As temperature can influence the reaction speed of lizards (Rand, 1964; Huey and Bennett, 1987), subjects were captured immediately after fleeing and body temperature was measured with a cloacal thermometer. Weight was measured with a Pesola scale (0-60 g) and snout-vent length was measured using a flexible ruler. Air temperature was recorded at 1.5 m above ground level. Two toes of each subject were clipped in different combinations so as to allow identification. Toe clipping is a standard field identification procedure for terrestrial lizards that has no detectable influence on behaviour (Dodd, 1993; Paulissen and Meyer, 2000; Husak and Fox, 2003).

Paint treatment: The lizards were captured and their capture locations marked. In this study, 94% of the lizards that were seen were captured, and these are the individuals on which the analyses are based. Experimental subjects were painted with non-toxic acrylic paint on dorsum, sides, head (avoiding parietal eye) and tail, either with brown or blue-turquoise, males (eight and 13, respectively) as well as females (11 and nine, respectively). White paint was used to mimic the small white spots covering the body. Paint colours were chosen to approximate, by eye, the actual colours of the lizards. Control subjects (six males and six females) were not painted. To allow visual identification, a unique number was painted on the right side of each subject with white paint.

Painted subjects were released at their locations of capture the following morning. One week after painting the lizards were recaptured to assess body weight as a physiological response to changes in predator approach frequencies associated with

alteration of conspicuousness (Martín and López, 1999a), and recapture frequency as an indication of predation pressure (Marler and Moore, 1988).

Behavioural adjustment to predation pressure: After a subject had shed its skin (within 5-6 weeks) and thus lost the paint (and the number used for visual identification), it was again approached to determine if anticipated changes in predator approach frequencies had affected subject wariness. Subjects were identified upon capture.

Local predator abundance: All sightings of potential *C. dickersonae* predators in the study area were recorded as an estimate of predation pressure on the study species.

RESULTS

Body features: Males were both larger (svl: 91 ± 0.9 (SE) mm) and heavier (36.3 ± 1.5 g) than females (svl: 80 ± 0.6 mm; t-test: $t = -9.899$, $p = 0.001$, $n\sigma = 36$, $n\phi = 26$; weight: 22.0 ± 0.8 g, t-test: $t = -8.529$, $p = 0.001$, $n\sigma = 36$, $n\phi = 26$). However, approach distance was not influenced by these body features (for males as for females: linear regressions: $r < 0.3$, $p > 0.05$, $n\sigma = 36$, $n\phi = 26$); neither was flight distance (for males, and for females: linear regressions: $r < 0.3$, $p > 0.05$, $n\sigma = 36$, $n\phi = 26$), nor scanning behaviour (for males as for females: linear regressions: $r < 0.2$, $p > 0.05$, $n\sigma = 22$, $n\phi = 8$). As size and weight did not influence anti-predation behaviour, they were not examined further.

Temperature: Body temperature did not differ between the sexes (male: 37.3 ± 0.32 (SE); female: 36.5 ± 0.46 ; t-test; $t = -1.419$, $p = 0.161$, $n\sigma = 36$, $n\phi = 26$), nor did it affect approach distance or flight distance (linear regression: $r < 0.3$, $p > 0.05$, $n\sigma = 36$, $n\phi = 26$). Male scanning behaviour was influenced marginally by body temperature (linear regression: $r = 0.399$, $p = 0.066$, $n = 22$) and significantly by air temperature (linear regression: $r = 0.645$, $p = 0.024$, $n = 11$); the males scanned more at higher temperatures. This influence was not observed for females (linear regressions: $r < 0.4$, $p > 0.05$, $n = 8$). Air-temperature did not affect approach distance (linear regressions: $r < 0.3$, $p > 0.05$, $n\sigma = 36$, $n\phi = 26$), although it had a significant, positive effect on male flight distance (linear regression: $r = 0.608$, $p = 0.016$, $n = 22$) it did not influence female flight distance (linear regression: $r = 0.022$, $p = 0.926$, $n = 22$).

1st capture: Before paint treatment

- i) Scanning: Scanning rate before the first capture did not differ between the sexes (males: median: 0.7, range: 0.0-2.2 scans/min; females: median: 0.8, range: 0.00-1.4 scans/min; Mann-Whitney U test: $U = 87.000$, $p = 0.982$, $n\sigma = 22$, $n\phi = 8$).
- ii) Pursuit deterrence signalling always consisted of the lizard moving in the direction of the observer, and was witnessed in only a few trials. Males (2/36)

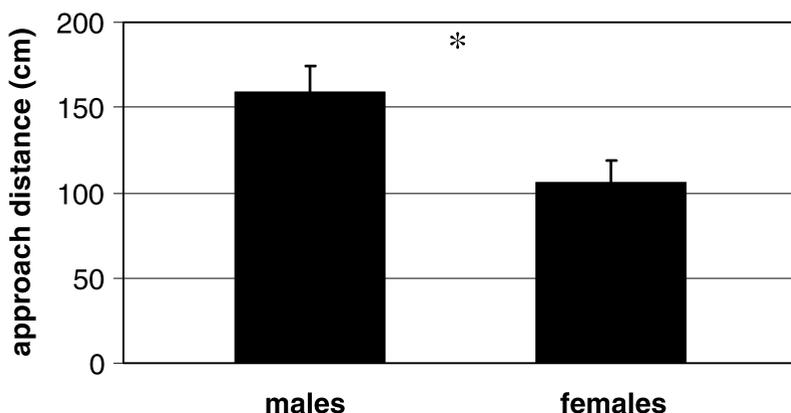


Figure 1. Mean approach distance (\pm SE) in cm of males and females that did not use refuge. The asterisk indicates a significant difference ($p < 0.05$).

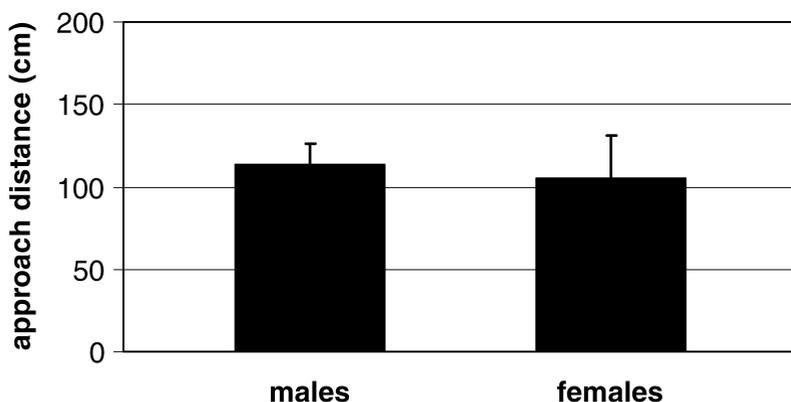


Figure 2. Mean approach distance (\pm SE) in cm of males and females that entered a refuge.

and females (1/26) do not differ in frequency of pursuit deterrence signalling ($\chi^2 = 0.096$, $p = 0.757$, $n\sigma = 36$, $n\varphi = 26$).

- iii) No aggression, threatening or imposing behaviours were observed.
- iv) Within subjects, approach distance and flight distance were neither correlated when subjects stayed out in the open (Pearson Correlation test: males: $r = 0.16$, $p = 0.492$, $n = 22$; females: $r = 0.34$, $p = 0.120$, $n = 22$) nor when they fled into refuge (Pearson Correlation test: males: $r = -0.076$, $p = 0.823$, $n = 11$; females: $r = 0.30$, $p = 0.702$, $n = 4$). Excluding subjects that used a refuge, females (106 ± 12.8 (SE) cm) allowed the predator to approach more closely before fleeing compared to males (159 ± 15.1 cm; t-test: $t = -2.679$, $p = 0.011$, $n\sigma = 22$, $n\varphi = 22$; fig. 1). In trials where subjects used a refuge, no sex difference was observed in approach distance between the sexes (males: 114 ± 12.5 cm, females: 105 ± 26.0 cm; t-test: $t = -0.336$, $p = 0.742$, $n\sigma = 13$, $n\varphi = 4$; fig. 2). Approach distance of males, but not females (t-test:

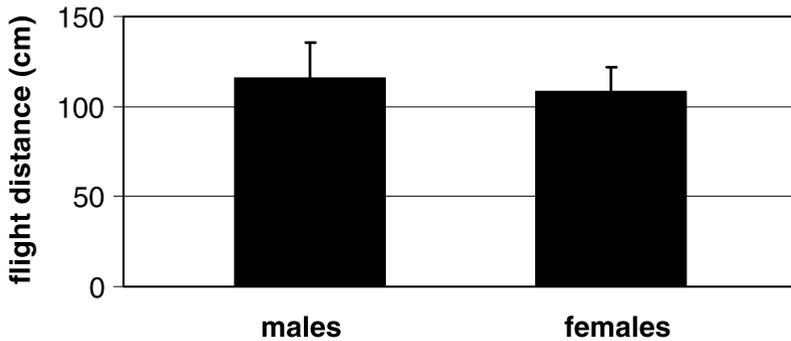


Figure 3. Mean flight distance (\pm SE) in cm of males and females that do not use refuge.

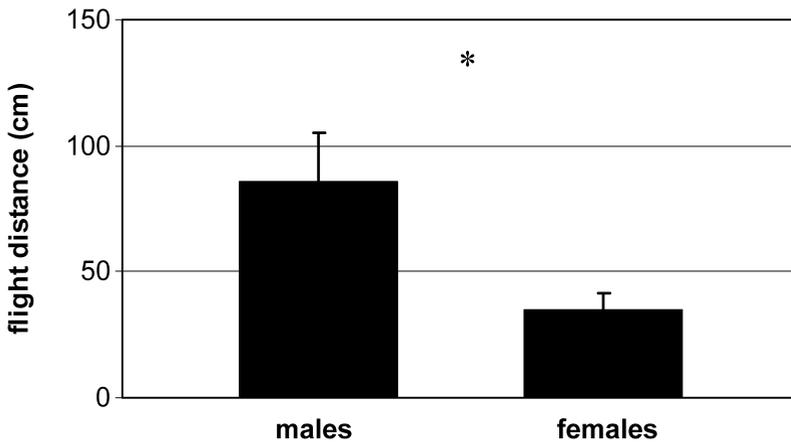


Figure 4. Mean flight distance (\pm SE) in cm of males and females that used a refuge. The asterisk indicates a significant difference ($p < 0.05$).

$t = 0.024$, $p = 0.983$, $n = 26$), tended to be shorter (i.e., they allowed a closer approach) when subsequently fleeing to refuge, compared to remaining in the open (t-test: $t = 1.945$, $p = 0.061$, $n = 35$).

- v) Flight distance did not differ between the sexes when subjects remained in the open (males: 116 ± 19.3 (SE) cm, females: 108 ± 14.0 cm; t-test: $t = -0.324$, $p = 0.748$, $n_{\sigma} = 22$, $n_{\varphi} = 22$; fig. 3). When refuge was used, however, flight distances of females (35 ± 6.5 cm) were shorter than those of males (86 ± 19.0 cm; t-test: $t = -1.504$, $p = 0.025$, $n_{\sigma} = 13$, $n_{\varphi} = 4$; fig. 4), and were shorter than when they remained in the open (t-test: $t = 4.728$, $p = 0.001$, $n = 26$).
- vi) Distraction behaviour consisted of zigzagging during flight or head bobbing immediately before or during flight. Four of the 36 male subjects displayed distraction behaviour at the first trial. Of these, one zigzagged and three made head bobs during flight. Only one of 26 females displayed distraction behaviour by zigzagging during flight. Males and females did not differ in the frequency

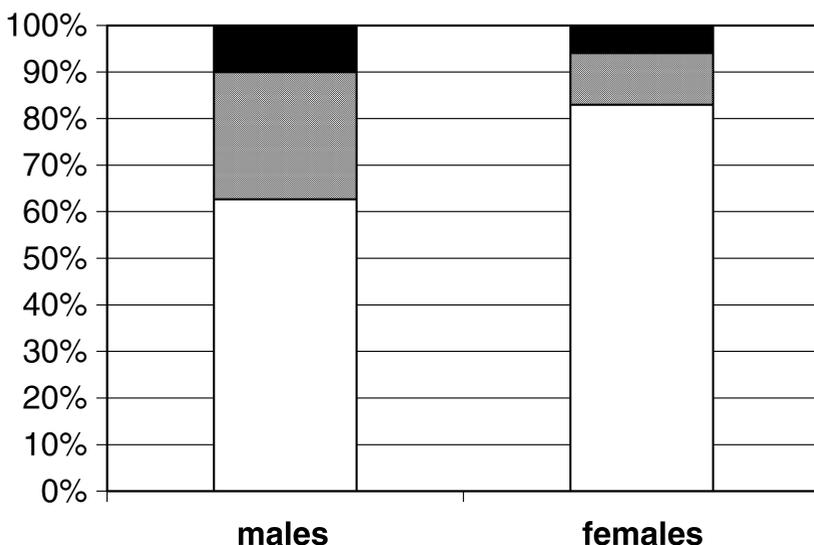


Figure 5. The percentage of males and females that fled under a rock (black), under a bush (grey) or stayed in the open (white).

with which they displayed distraction behaviour ($\chi^2 = 1.075$, $p = 0.300$, $n\sigma = 36$, $n\varphi = 26$).

- vii) Refuge consisted either of a bush with the lizard sitting close to the stem, or a rock where the lizard positioned itself so that it could watch the observer. Males fled to refuge in 13 of the 36 trials; ten males fled under a bush and three under a rock. Four of 26 females fled to refuge, of which three fled under a bush and one fled under a rock (fig. 5). Differences in the use of refuges between the sexes approached significance ($\chi^2 = 3.513$, $p = 0.061$, $n\sigma = 35$, $n\varphi = 26$).

2nd capture: Paint treatment

No significant differences in recapture frequency occurred following paint treatments (males: $\chi^2 = 5.712$, $p = 0.058$, $n = 6-13$; fig. 6; females: $\chi^2 = 1.88$, $p = 0.389$, $n = 6-11$; fig. 7), although a difference between blue-painted (five of 13 recaptured) and unpainted males (five of six recaptured) approached significance ($\chi^2 = 3.316$, $p = 0.069$, $n = 13$, $n = 6$, respectively). Males and females with the same paint treatment were recaptured at the same frequency (blue: $\chi^2 = 0.627$, $p = 0.429$, $n\sigma = 13$, $n\varphi = 9$; brown: $\chi^2 = 0.012$, $p = 0.912$, $n\sigma = 8$, $n\varphi = 11$; unpainted: $\chi^2 = 1.500$, $p = 0.221$, $n\sigma = 6$, $n\varphi = 6$). Paint treatments had no detectable effect on body weights (all treatments: paired t-test: $t < 1.6$, $p > 0.05$, $n = 3-8$), although the power to detect an effect in the paint treatment trials was low due to small sample sizes.

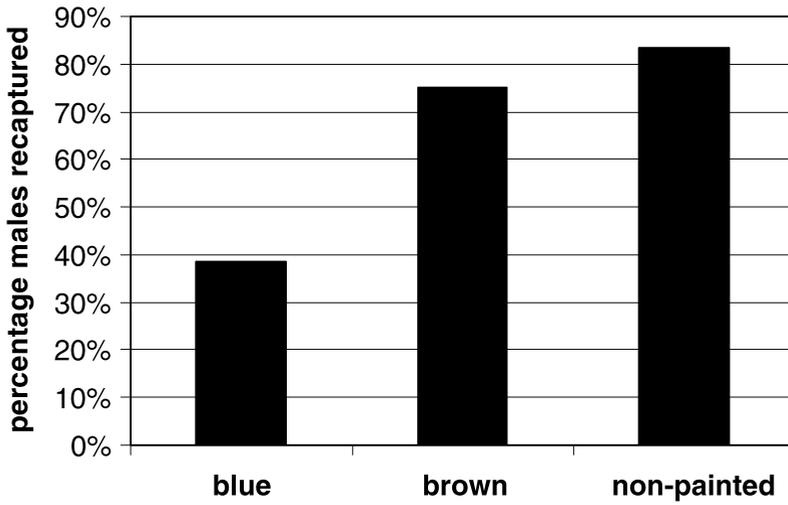


Figure 6. Recapture frequency of blue, brown and unpainted males.

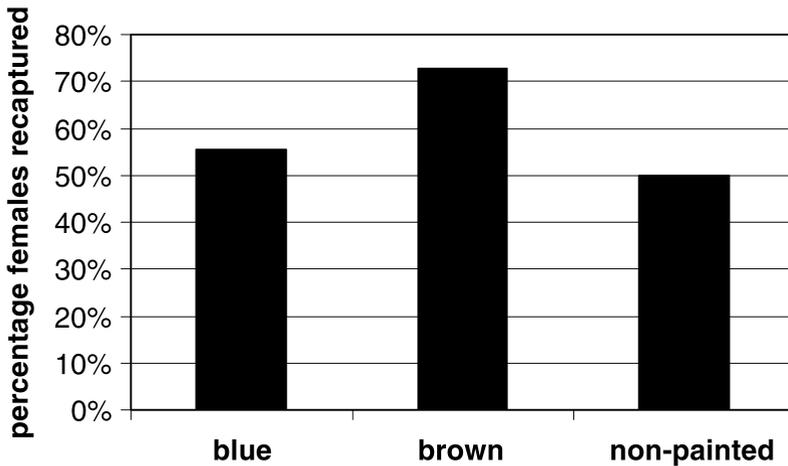


Figure 7. Recapture frequency of blue, brown and unpainted females.

3rd capture: After shedding painted skin

Scanning behaviour did not differ between the first sampling period (i.e., before the first capture) and that just prior to the third approach to the same males (Wilcoxon matched-pairs signed-rank test: $Z = -0.408$, $p = 0.683$, $n = 6$), although the power of the test is low. As scanning behaviour was not recorded in every trial for each female subject, all female subjects of the first approach were compared with all female subjects of the third approach. There was no difference in scanning rate of females in the first trial vs. the third trial (Mann Whitney U test: $U = 11.000$, $p = 0.461$, $n = 8, 4$). Males and females did not differ in scanning rates preceding the third approach (males: median: 1.1, range: 0.0-1.9 scans/min, females: median: 0.4,

range: 0.0-1.0 scans/min; Mann-Whitney U test: $U = 7.000$, $p = 0.154$, $n\sigma = 8$, $n\phi = 4$).

Lizards that were approached for a third trial did not use a refuge. Males exhibited significantly shorter approach distances in the third than the first trial (paired t-test: $t = 2.457$, $p = 0.034$, $n = 11$), but no differences in flight distance were detected in comparing the two trials (paired t-test: $t = -0.217$, $p = 0.832$, $n = 11$). For females, no differences in approach distance (paired t-test: $t = 0.209$, $p = 0.843$, $n = 6$) or flight distance were detected in comparing first and third trial (paired t-test: $t = -1.273$, $p = 0.259$, $n = 6$), although the power to detect an effect is low due to small sample sizes.

Only one of the 12 male subjects, and none of the six female subjects, displayed pursuit deterrence signalling, and no subjects displayed distraction behaviour.

Local predator abundance

From 7 May to 26 August 2005, the following potential predators of *C. dickersonae* were observed in the study area: seven hawks (*Buteo* spp.), 24 great horned owls (*Bubo virginianus*), five grey foxes (*Urocyon cinereo-argenteus*), two kit foxes (*Vulpes macrotis*), two Sonoran whipsnakes (*Masticophis bilineatus*), one black tailed rattlesnake (*Crotalus molossus*) and one sidewinder (*Crotalus cerastes*).

DISCUSSION

The question addressed in this study was whether bright blue Dickerson's collared lizard males differ in anti-predation behaviours from the less conspicuous brown females. Although in addition to coloration adult sexual dimorphism includes weight and size, these two variables did not appear to have a direct influence on anti-predation behaviour. Sex differences observed in *C. dickersonae* anti-predation behaviour might thus arise, at least in part, from the sexually dimorphic coloration of this species.

Temperature effects. Body temperature can influence the running speed of ectothermic animals (Rand, 1964; Christian and Tracy, 1981; Huey and Bennett, 1987). Temperature could therefore influence approach distance and flight distance, and temperature is even known to influence the success rate of hawk attacks on hatchling Galapagos land iguanas (*Conolophus pallidus*) (Christian and Tracy, 1981). Anti-predation behaviour in the study species did not appear to be influenced by body temperature, however. Neither escape speed nor sprint speed were quantified, but the lizards did not appear to flee at high speed. Air temperature influenced the flight distance of males negatively, i.e., males fled for shorter distances when air temperatures were high. This result could arise from thermal stress. Alternatively, subjects were more likely to be operating near their physiological optimum, which in turn would be expected to increase running performance and reduce reaction time.

These factors would be expected to reduce the distance placed between the subject and a potential predator after fleeing.

Scanning behaviour. Vigilant animals are less likely to be captured by predators. Differences in scanning rates between sexes were not observed, but air temperature and body temperature were correlated with scanning rate of males. Although greater success of predation on collared lizards would be anticipated when their body temperatures were lower, males scanned more at higher temperatures. This could be a general result of increased physiological efficiency, and a commensurate interest in interaction with conspecifics.

Scanning rate in the study species (about 0.7 scans per min) was low compared to that of birds: blackbirds and woodpigeons were observed to scan approximately 6-8 times per min (Fernández-Juricic et al., 2004). Scanning rate in these birds decreased to 3-4 times per min, however, in the absence of predators (Fernández-Juricic et al., 2004). If scanning rate can be considered a viable indicator of predation pressure, then the study species appears to experience little predation.

Pursuit deterrence signalling. The sole pursuit deterrence behaviour of the study subjects was to approach to the (simulated) predator. In the lizard *Anolis cristatellus*, approaching the predator (a model snake) was one of the three most frequent pursuit deterrence signals observed (Leal and Rodríguez-Robles, 1997). Approaching the predator also has been found to be effective anti-predation tactic in fish (Godin and Davis, 1995). As this behaviour is designed to draw attention of the predator to the potential prey, it should be costly and therefore honest (Grafen, 1990; Leal, 1999). In the present study pursuit deterrence was observed in only a few trials, and the sexes did not differ in display frequency. These results may indicate that the cost of fleeing is relatively low. Interestingly, males approached the (simulated) predator when females were nearby, and it has been argued that costs of fleeing can be increased when conspecifics are near (Cooper, 1999).

Imposing and aggression. No imposing or aggressive behaviour in response to the observer's approach occurred in the study species. Aggression toward predators can be dangerous and thus should be used by prey only when cornered (Hasson, 1991). The lizards did show aggression when captured, however, by turning and trying to bite the 'predator'.

Approach distance. The distance a subject allowed the observer to approach did not depend on the distance to refuge, as has been observed in some other lizard species (Bulova, 1994; Martín and López, 1995; Cooper, 2003). Approach distance of males was shorter in trials that included refuge use than when subjects remained in the open, however. Thus the use of refuge *per se* seems to be the important influence on approach distance. Predator density and prey conspicuousness should, of course, influence approach distance. A mainland population

of *Ctenosaura hemilopha*, for example, exhibited an average approach distance of over 30 m, whereas an island population with fewer predators allowed an average approach of 5.8 m (Blázquez et al., 1997). If predation pressure is greater on male *C. dickersonae* than on females, due to the males' greater conspicuousness, approach distances should be longer in males than in females. When *C. dickersonae* males did not use refuge, they exhibited significantly longer approach distances than females. This result is consistent with those of Heatwole (1968) on *Anolis stratulus* and *A. cristatellus*; the latter being less cryptic and exhibiting longer approach distances. Last, approach distance in *C. dickersonae* is short (1.1-1.6 m) compared to the smaller Sonoran Desert lizards *Callisaurus draconoides* (5.6-8.8 m) and *Cophosaurus texanus* (3.6-5.0 m) (Bulova, 1994), and to the much larger iguana *Ctenosaura hemilopha* (5.8-30 m) (Blázquez et al., 1997). If approach distance is a viable indicator of predation intensity, then *C. dickersonae* appears to experience comparatively weak predation pressure.

Flight distance. When no refuge was used, flight distance did not differ between the sexes. However, when subjects felt threatened enough to flee to refuge, males fled further than females. The sex difference may indicate that effective refuges for males and females differ due to differences in body size and in conspicuousness.

Distraction behaviour. Head bobbing or zigzagging during flight might be viewed as behaviours aimed at distracting or confusing a predator. Males and females displayed this behaviour equally, but only rarely. Distraction behaviour has been considered most useful when prey are inconspicuously coloured and engage in a conspicuous display that is followed immediately by fleeing and stopping suddenly (Hasson, 1989; "flash-concealment" of Leal and Rodríguez-Robles, 1997). Such behaviour would not seem to be an effective anti-predation tactic for adult male *C. dickersonae*, however, given their conspicuous coloration.

Refuge use. Refuge use can be expected to increase with increased predation pressure (Martín and López, 1999a). Male *C. dickersonae* tended to use refuge more often than did females when approached by the observer. Lizards that fled under a rock usually came out from under it within seconds. Most often refuge was a bush where the lizard sat close to the stem. Bushes may be protective against aerial predators, but the open bushes in the study area would be unlikely to deter terrestrial predators. Most of the subjects did not go to cover, perhaps because certain costs are associated with refuge use. For example, time spent in refuge might otherwise be used for foraging or interactions with conspecifics (Ydenberg and Dill, 1986). Ectothermic animals (like the study species) that flee into refuge will lose their preferred temperature (Martín and López, 1999b), influencing their performance negatively (Huey, 1982). Moreover, when in refuge the prey may lose sight of the predator (Lima and Dill, 1990) and emergence from hiding can be lethal if the

predator is still near. Given that the most commonly used refuge in this study was that of open bushes, subjects could continue to monitor the observer while in refuge.

Painting treatment. If individuals are not migrating, the percentage of individuals recaptured can serve as a rough indicator of predation pressure (Marler and Moore, 1988). Although few differences among paint treatments were observed, fewer blue-painted males were recaptured than unpainted males. Males are only at their brightest coloration at preferred (high) body temperature, however, and are thus less conspicuous at lower temperatures early in the morning when the chance of encountering a predator is highest (i.e., crepuscular and some nocturnal predators may still be active). In contrast, blue-painted subjects were conspicuous at all times of day. Blue painted subjects therefore could have suffered more from predation.

Martin and López (1999a) suggested that weight loss in wall lizards painted to be conspicuous was likely due to spending increased amounts of time fleeing and hiding from predators. Body weight was not altered in *C. dickersonae* subjects by the paint treatments, however. Overall recapture rate was high (up to 80%) compared to some other studies (Martín and López, 2001), again suggesting a low impact of predation pressure on the study species.

Behavioural adjustment to predation pressure. Selection favours animals that learn quickly to avoid predators (Marcelini and Jenssen, 1991). No change in approach distance, flight distance, or other recorded anti-predation behaviour was observed in subjects that were approached a third time. The fact that subjects did not become more wary to being captured repeatedly may be yet another indicator of historically weak predation pressure on the study species. Alternatively, habituation of subjects to the observer's presence over time may have offset any short-term changes associated with the trauma of being captured and painted.

Local predator abundance. The most dangerous avian predators of *Crotaphytus* sp. are the roadrunner (*Geococcyx californianus*) and potentially hawks (*Buteo* sp.), whereas the most dangerous snake predator is the coachwhip (*Masticophis flagelum*) (Husak et al., 2005). Birds and coachwhips have excellent colour vision and should be able to detect *C. dickersonae* males readily. Although the distribution of these predators includes the western Sonoran Desert, no roadrunners or coachwhips were observed during the study and comparatively few sightings of hawks were made.

The most frequently seen predator was the great horned owl (*Bubo virginianus*: 24 sightings). This large avian predator was active during the day in the study area, but how much of a threat it represents to the collared lizards is unknown. Only 7-8% of the photoreceptors in the owl eye are cones (Fite, 1973) so its colour vision is likely to be poor. Such a visual system would be better adapted to seeing moving prey (such as rodents) than to detecting collared lizards, which spend much of their time perched immobile on rocks. This argument applies as well to the foxes observed on

occasion in the study area, which, as nocturnal/crepuscular carnivores, are likely to possess highly rod-biased visual systems and poor colour vision.

The lack of evidence for substantial predation pressure in the present study suggests that the advantages of conspicuous male coloration in male-male interactions and in mate attraction must outweigh the disadvantages of increased visibility to predators. Predation pressure likewise has been argued to modulate the evolution of sexually selected conspicuous coloration in populations of *C. collaris* (Baird et al., 1997). In the western United States, for example, whereas species richness and local abundance of *C. collaris* predators (and small lizards preyed upon by collared lizards) increases along a north-south latitudinal gradient, *C. collaris* colour conspicuousness decreases along the same gradient (Macedonia et al., 2002). Eight of the nine recognised collared lizard species have distributions that include Mexico (McGuire, 1996), but *C. dickersonae* is the only Mexican species in which one sex (males) exhibits highly conspicuous body coloration. Although no attempt has been made to quantify predation pressure in other Mexican collared lizards, evidence from the present study suggests that it is weak in *C. dickersonae*. Investigation of the enigmatic coloration of this species is ongoing, and future work will include analyses of *C. dickersonae* colour conspicuousness from the perspectives of conspecific and predator visual systems.

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