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**Choosing between a rock and a hard place: Camouflage in the round-tailed horned lizard *Phrynosoma modestum***

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**Abstract** The round-tailed horned lizard *Phrynosoma modestum* is cryptically colored and resembles a small stone when it draws legs close to its body and elevates its back. We investigated effectiveness of camouflage in *P. modestum* and its dependence on stones by placing a lizard in one of two microhabitats (uniform sand or sand with surface rocks approximately the same size as lizards). An observer who knew which microhabitat contained the lizard was asked to locate the lizard visually. Latency to detection was longer and probability of no detection within 60 s was higher for lizards on rock background than on bare sand. In arenas where lizards could choose to occupy rock or bare sand, much higher proportions selected rocky backgrounds throughout the day; at night all lizards slept among stones. A unique posture gives *P. modestum* a rounded appearance similar to many natural stones. Lizards occasionally adopted the posture, but none did so in response to a nearby experimenter. Stimuli that elicit the posture are unknown. That *P. modestum* is better camouflaged among rocks than on bare sand and prefers to occupy rocky areas suggests that special resemblance to rocks (masquerade) enhances camouflage attributable to coloration and immobility [*Current Zoology* 58 (1): – , 2012].

**Keywords** Animal defense, Background matching, Camouflage, Crypsis, Masquerade, Squamata

Camouflage has the primary effect of rendering exposed prey more difficult to detect by predators (Edmunds, 1974; Ruxton et al., 2004). It operates by several mechanisms, some well established and others only now beginning to be investigated critically (Cott, 1940; Edmunds, 1974; Ruxton et al., 2004; Skelhorn et al., 2010a,b). Eucrypsis has long been recognized in diverse prey that blend with their habitat by matching the background coloration (Cott, 1940). Masquerade, also known as special resemblance, is a less common means of avoiding being recognized as prey by having the appearance of an inanimate object (Edmunds, 1974; Ruxton et al., 2004). Prey may be camouflaged by being cryptic, by masquerade, or both (Skelhorn et al., 2011).

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In complex natural habitats where multiple backgrounds having different visual characteristics are present, prey are likely to be more detectable on some backgrounds than others. Some prey that occupy various microhabitats having different background coloration and contrast maintain crypsis by changing color to match the current background (e.g., Kats and Van Dragt, 1986; Langridge, 2006; Vokey and Burton, 1998). Crab spiders decrease detectability by selecting background coloration on the basis of their current color (Heiling et al., 2005).

For camouflage to be effective in species lacking these abilities, prey should actively choose to occupy microhabitats where they are inconspicuous. Behavioral background matching occurs in some eucryptic prey (Ergene, 1950; Manríquez et al., 2008; Morey, 1990; Sargent, 1968). Relatively little is known about behavioral maintenance of masquerade through habitat selection, but it occurs in a caterpillar (Herrebut et al., 1963, Greene, 1989; Skelhorn et al., 2011). For vertebrate prey that masquerade as inanimate objects, preferences for microhabitats where the object being mimicked is present have not been investigated. The round-tailed horned lizard *Phrynosoma modestum*, which is sexually monomorphic in general appearance, is believed to masquerade as a stone (Sherbrooke, 2003; Sherbrooke and Montanucci, 1988). Similarity to a stone is greatest when a lizard's ventrum is on the ground, its legs are tucked against its body, and its back is curved upwards, giving the lizard a rounder form contrasting with the typical flat body shape of horned lizards (Merilaita, 2003; photos in Sherbrooke, 2003; Cooper and Sherbrooke, in press). In this pose, *P. modestum* appears to protrude above its smooth background surface, casting a stone-like shadow enhanced by dark lateral coloration and lack of lateral fringe scales that contribute to camouflage in other species of *Phrynosoma* by disrupting shadow-outlining of the body (Sherbrooke and Montanucci, 1988).

Camouflage in *P. modestum* might have several components. First, eucrypsis due to inconspicuous coloration is highly developed in horned lizards (Norris and Lowe, 1964; Sherbrooke, 2003). In *P. modestum* the dorsal color patterns vary geographically, matching local substrate colors (Bundy and Neess, 1958), and may be polymorphic at single localities (Sherbrooke and Montanucci, 1988). Such polymorphism might be adaptive for masquerading prey due to by enhancing crypsis as well as by increasing the scarcity of masqueraders relative to models (Skelhorn and Ruxton, 2010; Skelhorn et al., 2011), but it is unclear whether polymorphism within a single area having varied substrates in *P. modestum* is accompanied by substrate selection that enhances crypsis. Second, special resemblance to small rocks makes *P. modestum* difficult to detect when immobile (Sherbrooke and Montanucci, 1988; WEC and WCS, personal observations). Third, background matching is enhanced by physiological color change that lightens the skin at mid-day and darkens it near sunrise and before sunset (Sherbrooke and Frost, 1987; Sherbrooke, 1997). Fourth, behaviours such as habitat selection and immobility might decrease probability of being detected. Camouflaged prey can and do reduce their detectability by remaining immobile (Broom and Ruxton, 2005; Cooper et al., 2008). We predicted that *P. modestum* is more difficult to detect in microhabitats where small rocks occur and preferentially occupies rocky microhabitats where it is cryptic. Finally, *P. modestum* might adopt the rounded posture with elevated dorsum and tucked legs to enhance camouflage when a predator is nearby.

To assess the effectiveness of camouflage, assess whether background selection contributes to it, and ascertain whether *P. modestum* adopts a rock-like posture in response to nearby predators, we conducted three experiments. In the first we measured difficulty for human observers to detect *P. modestum* on backgrounds of small stones on sand and on uniform sand. In the second experiment we tested the hypothesis that *P. modestum* selectively occupies a background where it is camouflaged. The final experiment tested the hypothesis that *P. modestum* adopts the putatively stone-mimicking posture when a predator moves nearby. We predicted that lizards would be more difficult to detect on a background of small stones than on sand due to masquerade or environmental complexity (Merilaita, 2003) and that

lizards would select the background on which they were less conspicuous. Because *P. modestum*'s rock-like posture is believed to enhance masquerade, we assessed the effect of human presence on adoption of the posture. No prediction was made because stimuli that induce adoption of the posture are unknown.

## 1 Materials and Methods

### 1.1 Collection, maintenance, and experimental sites

Twenty-one adult *P. modestum* were collected in Hidalgo County, New Mexico between 23 May and 8 June of 2009 and were transported to the American Museum of Natural History's Southwestern Research Station near Portal, Arizona. They were housed under natural photothermal conditions in an outdoor pen in the Animal Behavior Observatory. Lizards were sprinkled with water to allow rain-harvesting from their dorsal surfaces (Sherbrooke, 1990a). They were fed domestic crickets *Acheta domesticus* supplemented by seed-harvester ants *Pogonomyrmex* spp..

Data were collected on in June, 2009 at temperatures 22-29 °C. Two brief intervals of rain occurred during the substrate selection experiment during which no data were collected, but the weather was sunny otherwise. The experiments on detectability and substrate selection were conducted in large wire-covered enclosures (7.0 × 3.8 × 2.4 m lwh) having sand substrates and unclimbable sheet-metal walls (0.6 m high) for the experiments on degree of crypsis and in a similar enclosure (4.3 × 1.7 × 2.4 m lwh) for experiments on microhabitat selection).

### 1.2 Detectability on substrates by human observers

One end of the large enclosure was a wall of the Animal Behavior Observatory that had a door allowing access to the enclosure and a one-way viewing window for observations. In each trial a lizard was placed in a 3.0 × 1.9 m area that contained uniform sand or sand with stones arranged at evenly spaced intervals. To assess effects of presence of rocks on detectability of *P. modestum*, we recruited seven human volunteers from people at the Southwestern Research Station during the study. All were in their late teens to twenties and were naïve regarding field collection of horned lizards. No attempt was made to assess the visual acuity or color vision of the observers.

Natural predators of horned lizards include mammals, especially canids, birds, and snakes (Sherbrooke, 1990b; 2008; Middendorf and Sherbrooke, 1992; Sherbrooke and Middendorf, 2004). Thus, their predators have variable visual capacities including the spectral range of human beings plus the near ultraviolet wavelengths visible to snakes and birds. Our study cannot rule out the possibility that *P. modestum* is conspicuous in the near ultraviolet, but is adequate to assess camouflage over a wide range of hue and brightness. Human observers have been used successfully to study crypsis and conspicuousness of lizards and frogs (Cuadrado et al., 2001; Cooper et al., 2008, 2009).

Before an observer's first trial, the observer was told and shown where to stand facing away from the area where a lizard would be placed and looking at an opaque wall. The observer was also told that he would be instructed when to turn to area containing a lizard and begin to search for it visually without any further movements, and to point to the lizard and say that he had detected it if and when he detected it. The observer was also informed that each trial would last no longer than 60 s. Before each trial the observer was told whether the lizard would be on open sand or among rocks. To begin a trial, an observer (volunteer) who knew whether the lizard would be placed on open sand or among rocks stood adjacent to and facing the solid wall while WEC placed a lizard. After placing a lizard in the observation

area, WEC moved to the wall and told the volunteer to begin. The volunteer then turned to search for the lizard while remaining next to the wall. Both the observer and WEC remained motionless during the trial. The volunteer indicated verbally and by pointing when he or she had detected the lizard. WCS remained out of view inside the Animal Behavior Observatory and recorded latency to detection. If the observer did not detect the lizard within 60 s, latency for that trial was recorded as 60 s. Lizards on sand were almost all detected in less than 30 s, but those on rock were typically undetected within than time. However, if a lizard moved, it was typically detected immediately. To avoid artificial reduction of latency to detection due to movement that would obscure a difference between groups, a trial was discarded if the lizard moved in less than 30 s., The trial was repeated. If detection due to movement occurred between 30 and 60 s, the latency to detection was recorded conservatively as if no movement had occurred. Ten consecutive trials were conducted for each observer on 24 June, 2009, with background type alternated between trials. In the first trial the lizard was among rocks for four observers and on bare sand for the other three.

Two aspects of the experimental procedure require comment. First, the observer stood during trials. Natural predators such as snakes and canids are not as tall as human beings, but the latter are tall enough to be readily detectible at a distance. Furthermore, avian predators may be perched at a range of heights including and exceeding the height of observers. It is clear from our laboratory and field observations that the lizards often orient themselves toward a human observer's face. Second, because observers indicated that they had detected lizards by pointing at them, it is possible that some false positive detections occurred. However, this is highly unlikely because after detection was indicated by pointing, observers were allowed to move to verify detection.

The proportion of number of observers who detected more lizards on bare sand than among rocks was tested for significance using a binomial test. Sign tests were used to examine the possibilities that latency to detection decreased between first and last trials and that more lizards would be detected only after moving when among rocks than on sand. Effect size for sign and binomial tests is  $g = 0.5 - P$ , which has a maximum value of 0.50 (Cohen 1992). The effects of microhabitat type and differences among observers on latency to detection were examined using a 2 x 2 factorial analysis of variance. Because latency to detection had a nonnormal distribution due to frequent failure to detect lizards on the rocky area, the analysis was conducted using ranks of latency to detection. The effect sizes are reported as  $\eta^2$ , which may be interpreted like  $R^2$  (Cohen, 1992).

### 1.3 Substrate selection by lizards

The experimental enclosure was divided into two halves, each  $2.1 \times 1.7$  m. Rocks close to the size of the lizards (3–5 cm) were arranged on the sand in one half in a  $16 \times 21$  array with intervals of 9.4 cm between rows and 10.2 cm between columns of rocks. The other half of the enclosure had a uniform sand substrate. At 0830, 20 lizards were placed at the rock-sand interface. The experimenter then left the area. At 30 minute intervals between 09: 00 and 16: 00 h Mountain Standard Time, the experimenter quietly approached the enclosure and recorded the number of lizards on each half of the enclosure. Data were not collected for two intervals when it was raining. Binomial tests were conducted for each observation time to test for preference for rocks versus open sand. Because eleven binomial tests were conducted, one for each interval, significance tests were conducted using lowered  $\alpha$  values according to a sequential Bonferroni procedure (Wright, 1992). To examine nighttime microhabitat selection, we placed 20 lizards in the same enclosure during the daytime on a different day and recorded their locations on the rock or sand half of the enclosure in the morning before lizards had become active. A binomial test was used to assess the significance of the difference in proportion of lizards occupying each half of the enclosure. Data on substrate selection were collected in late June after

the other experiments had been completed. In these experiments, substrate was confounded with location because one side of the enclosure always contained rocks, whereas the other side contained no rocks. We do not believe that this affected the outcome for two reasons. Lighting was very similar on the rocky and sandy sides throughout the observation interval. Second, lizards in similar enclosures lacking rocks distribute themselves throughout the enclosures.

#### 1.4 Postures enhancing masquerade or crypsis

To examine whether the lizards adopt postures that enhance crypsis or masquerade, including lying flat on the ground and the stone-like posture, we placed groups of five lizards in the rocky area on 14 June, 2010, and moved out of their sight for five minutes. After five minutes, WEC entered the enclosure and walked about it, staying out of the rocky area and neither directly approaching nor gazing at lizards. Four replicate groups were observed. We recorded any changes in the two postures or the absence of change.

## 2 Results

### 2.1 Detectability on substrates by human observers

Numbers of lizards that were not detected within 60 s when among rock and on open sand were (3,0), (3,0), (5,0), (1,0), (2,0) (2,1), and (5,2) for each observer and (21,3) for all observers pooled. The observer who failed to detect one lizard on sand later said that he thought it was a rock; another observer detected a lizard on sand and initially asked if it were a rock before identifying it as a lizard. For each of the seven observers, the number of trials in which lizards not detected was greater for lizards among rocks than on open sand, indicating that detection was significantly more likely on open sand (binomial test,  $P = 0.016$ ,  $g = 0.48$ ).

For data pooled among all observers, the proportion of trials in which individuals were detected on sand ( $0.91 \pm 0.04$ ) was almost twice as large as the proportion of trials in which they were detected among rocks ( $0.40 \pm 0.08$ ). Among lizards that were detected, some were detected only when they moved (8 of 15 among rocks, 1 of 34 on open sand). Because these cases were distributed among only six observers (five only for rock, one only for sand) the trials were not independent. Under the one-tailed hypothesis that more lizards among rocks would be detected only when they moved because they are more cryptic among rocks than on sand, the difference is not significant (sign test,  $P = 0.11$ ;  $g = 0.39$ ). Because the sign test has artificially high power due to the lack of independence among observers, but even so was not significant, there is no evidence that lizards among rocks were more likely to be detected only upon moving than lizards on sand.

Latency to detection was longer for lizards among rocks than on bare sand for each of the observers, and these differences were large (Fig. 1). Because so many lizards were not detected within 60 s, the distribution of latency to detection was nonnormal. In an analysis of variance by rank of latency, observers differed significantly in speed of

detection ( $F_{6,56} = 2.90, P = 0.016$ ). This difference is apparent in the longer times required to detect lizards by observer 7 than by observers 2 and 6. Latency to detection was significantly longer when lizards were among rocks than on open sand ( $F_{1,56} = 80.85, P < 1.0 \times 10^{-6}$ ; Fig. 1). The effects sizes were  $\eta^2 = 0.11$  for observer and  $\eta^2 = 0.50$  for substrate. The interaction between observer and substrate was not significant ( $F_{6,56} = 1.20, P > 0.10$ ).

## 2.2 Substrate selection by lizards

When given a choice of occupying an area of open sand or an area of stones approximately the same size as lizards, the lizards exhibited a strong preference for the area with stones. Lizards moved throughout the day, providing ample opportunity for all individuals to redistribute themselves between observation times. For 20 lizards observed 11 times each, lizards were on the rocky area in 185 trials, on open sand in 32 trials, and at the interface of these areas in 3 trials. In eight of the 11 times at which the lizard distributions were recorded, significantly more lizards were on the area with stones than on the open sand (Table 1). Effect sizes often were near the theoretical maximum of 0.50 (Table 1).

In a separate test all of 20 individuals placed in an enclosure in the afternoon slept in the rocky area rather than the area of open sand. This difference was highly significant (binomial test,  $P < 0.0001$ ) with a very large effect size  $g = 0.50$ .

## 2.3 Postures enhancing crypsis or masquerade

In the four trials in which groups of five lizards were in the test arena for five minutes, all 20 individuals were standing when an investigator walked nearby, but not directly toward lizards. None of them responded to the investigator's presence and movement by flattening against the substrate or adopting the posture putatively used for masquerading as a stone.

# 3 Discussion

## 3.1 Camouflage

Round-tailed horned lizards are effectively camouflaged when among rocks on sand. This was demonstrated by the much longer latency to detection of lizards among rocks than on sand lacking rocks and by the frequent inability of observers to detect a lizard among rocks even though they knew that one was present in a relatively small area. These findings are consistent with adaptive resemblance to stones, but alternative untested hypotheses, such as habitat complexity (Merilaita, 2003) might account for the longer latency to detection of lizards among rocks than on open sand.

We are uncertain about the extent to which the observed camouflage is due to crypsis or masquerade, but both are presumably important. *Phrynosoma modestum* is eucryptic, having inconspicuous dorsal coloration that varies geographically in a manner matching variation in background coloration (Bundy and Neess, 1958; Norris and Lowe, 1964; Sherbrooke, 2003). That the lizards were more readily detected among stones on sand than on open sand of the same color shows that the lizards are harder to detect among rocks. This shows that rocks contribute to camouflage and suggests, but does not demonstrate, that the lizards masquerade as stones.

The degree of camouflage of *P. modestum* to natural predators having visual systems that differ substantially from that of human beings, especially birds and snakes that see near ultraviolet wavelengths invisible to people (Sillman et al., 1997; Stuart-Fox et al., 2006), is unknown. However, horned lizards frequently remain immobile when approached by

birds and snakes (Sherbrooke, 1990b, 2008). Furthermore, roadrunners *Geococcyx californianus* have difficulty locating immobile horned lizards (Sherbrooke, 1990b). These data strongly suggest that *P. modestum* is camouflaged to avian and ophidian predators. Presumably their camouflage is effective against mammals, such as their natural canid predators (Middendorf and Sherbrooke, 1992; Sherbrooke and Middendorf, 2004), that have dichromatic color vision rather than the trichromatic color vision of people (Neitz et al., 1989). However, predators having dichromatic visual systems need not have inferior ability to detect lizards, and might have greater ability to do so. This is suggested by the superior ability of color-blind capuchin monkeys to detect camouflaged insects (Melin et al., 2007).

### 3.2 Microhabitat selection

Given that lizards were more difficult to detect when among rocks, the strong preference for the rocky microhabitat should enhance their ability to masquerade as rocks. Although lizards moved frequently throughout the day, they left the rocky area infrequently. Even after the first half hour during which basking occurred, three fourths of the lizards were in the rock microhabitat. At all other times an even higher proportion of lizards chose the rocky area with the exception of 14:00 MST when it was cloudy and humid after a brief rain. The degree and consistency of selection of rocky backgrounds shows that *P. modestum* preferentially occupy a microhabitat where they are difficult to detect. The mechanism of microhabitat selection remains unknown, but is likely to be visually mediated because horned lizards, like other iguanians, (1) have highly developed vision (Loew et al., 2002), and (2) like other phrynosomatids, have relatively poorly developed vomeronasal systems and do not rely on lingually sampled chemical cues to locate or identify food (Cooper, 1994, 1995, 1997; Cooper and Sherbrooke, 2009).

The strong preference for landscapes containing rocks roughly as large as the lizards themselves suggests that *P. modestum* maximizes the effectiveness of masquerade by adaptive microhabitat selection. Occupation of areas where they are camouflaged suggests that increased survival of individuals at rest among small stones favored active selection of areas where stones occur. Similar preferences are known in cryptic prey that select background coloration, e.g., grasshoppers (Gillis, 1982), moths (Kettlewell and Conn, 1977), spiders (Heiling et al., 2005), lizards (Vetter and Brodie, 1977), or match it by color change, e.g., cephalopods (Langridge, 2006), fish (Vokey and Burton, 1998), frogs (Kats and Dragt, 1986). Behavioral background matching must be very widespread among vagile prey if camouflage is to be effective.

In addition to selecting the rocky area during daytime hours of activity, round-tailed horned lizards uniformly selected the area with rocks to spend the night. Occupying the rocky area at night conceivably could increase camouflage with respect to nocturnal predators, especially on nights with bright moonlight. Although some horned lizards, including round-tailed horned lizards (WEC and WCS, personal observations) often spend the night buried beneath the sand, reducing the need for any such advantage, this behaviour may vary between species and with local soil conditions (Sherbrooke, 2003). On the other hand, individuals that selected substrates littered with small rocks might gain advantages due to masquerade before nightfall, and would be camouflaged in the morning as soon as light intensity increased for lizards that stayed on the surface overnight or upon emergence for those that buried themselves in the sand.

Although we have interpreted selection of a rocky substrate in terms of its implications for masquerade, other reasons for the observed microhabitat selection might include attraction to food found among rocks, decreased accessibility to predators, and thermoregulatory advantage. These factors, however, are unlikely to affect microhabitat selection. Rocks similar in size to lizards rarely have crevices used by insects eaten by *P. modestum*, which is an ant specialist that consumes ants foraging on the surface (Sherbrooke, 2003). Both rocks and lizards are too small for rocks to block access by predators. Although rocks might retain heat longer than sand, the rocks used in this study were very

unlikely to provide any benefit for thermoregulation because they were separated by open sand and lizards did not lie on rocks and rarely touched them during trials. The most likely explanation of selection of rocky substrates is enhancement of masquerade.

### 3.3 Postures that enhance camouflage

The failure of lizards to adopt the flattened posture or the posture believed to enhance resemblance to stones (Sherbrooke, 2003; Sherbrooke and Montanucci, 1988) when an investigator walked nearby may indicate that lizards do not adopt the posture upon detecting approaching predators at short range. The possibility that the lizards did not perceive the researchers as potential predators is not credible because *P. modestum* and *P. cornutum* vary their escape behaviour in relation to degree of predation risk posed by approaching people in accordance with escape theory (Cooper and Sherbrooke, 2010a, b, in press). If the increase in risk of being detected due to movements (Cooper et al., 2008; Cott, 1940) required to flatten on the substrate or elevate the dorsum and tuck the legs is great enough, any benefit of the posture would be negated and overall risk could increase. An alternative explanation for failure to adopt the posture could be that frequent exposure to people during and before the experiments induced habituation. We have no evidence that the lizards adopt the stone-like posture in response to the presence of predators in the field or in the laboratory. They sometimes used the posture during our studies, but we did not discover stimuli that elicited it. Studies of the effect of presence of stones in the absence of nearby predators on adoption of the posture would be of interest.

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## References

- Broom M, Ruxton GD, 2005. You can run or you can hide: Optimal strategies for crypic prey against pursuit predators. *Behavioral Ecology* 16: 534–540.
- Bundy RE, Neess J, 1958. Color variation in the round-tailed horned lizard, *Phrynosoma modestum*. *Ecology* 39: 463–477.
- Cohen J, 1992. A power primer. *Psychological Bulletin* 112: 155–159.
- Cooper WE, Jr., 1994. Chemical discrimination by tongue-flicking in lizards: A review with hypotheses on its origin and its ecological and phylogenetic relationships. *Journal of Chemical Ecology* 20: 439–487.
- Cooper WE, Jr., 1995. Foraging mode, prey chemical discrimination, and phylogeny in lizards. *Animal Behavior* 50: 973–985.
- Cooper WE, Jr., 1997. Correlated evolution of prey chemical discrimination with foraging, lingual morphology, and vomeronasal chemoreceptor abundance in lizards. *Behavioral Ecology and Sociobiology* 41: 257–265.
- Cooper WE, Jr., Sherbrooke WC, 2009. Prey chemical discrimination by tongue-flicking is absent in the Texas horned lizard *Phrynosoma cornutum*. *Journal of Herpetology* 43: 688–692.
- Cooper WE, Jr., Sherbrooke WC, 2010a. Initiation of escape behavior by the Texas horned lizard *Phrynosoma cornutum*. *Herpetologica* 66: 64–71.



- Cooper WE, Jr., Sherbrooke WC, 2010b. Plesiomorphic escape decisions in cryptic horned lizards *Phrynosoma* having highly derived antipredatory defenses. *Ethology* 116: 920–928.
- Cooper WE, Jr., Sherbrooke WC, In press. Crypsis influences escape decisions in the round-tailed horned lizard *Phrynosoma modestum*. *Canadian Journal of Zoology*
- Cooper WE, Jr., Caldwell JP, Vitt LJ, 2008. Effective crypsis and its maintenance by immobility in *Craugastor* frogs. *Copeia* 2008: 527–532.
- Cott HB, 1940. *Adaptive Coloration in Animals*. London: Methuen.
- Cuadrado M, Martin J, Lopez P, 2001. Camouflage and escape decisions in the common chameleon *Chamaeleo chamaeleon*. *Biological Journal of the Linnean Society* 72: 547–554.
- Edmunds M, 1974. *Defence in Animals*. Harlow, Essex, UK: Longman.
- Ergene S, 1950. Wälen Heuschrecken ein homochromes Milieu? *Deutsche Zoologisches Zeitschrift* 1: 122–132.
- Gillis JE, 1982. Substrate colour-matching cues in the cryptic grasshopper *Circotettix rabula rabula* (Rehn & Hebard). *Animal Behaviour* 30: 113–116.
- Greene, E, 1989. A diet-induced developmental polymorphism in a caterpillar. *Science* 243: 643–646.
- Heiling AM, Chittka L, Cheng K, Herberstein ME, 2005. Colouration in crab spiders: Substrate choice and prey attraction. *Journal of Experimental Biology* 208: 1785–1792.
- Herrebut WM, Kuytan PJ, de Ruiter L, 1963. Observations on colour patterns and behavior of caterpillars feeding on Scots pine. *Archives Néerlandaises de Zoologie* 15: 315–357.
- Kats LB, Van Dragt RG, 1986. Background color-matching in the spring peeper *Hyla crucifer*. *Copeia* 1986: 109–115.
- Kettlewell HBD, Conn DLT, 1976. Further background-choice experiments on cryptic Lepidoptera. *Journal of Zoology* 181: 371–376.
- Langridge KV, 2006. Symmetrical crypsis and asymmetrical signalling in the cuttlefish *Sepia officinalis*. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 273: 959–967.
- Loew ER, Fleishman LJ, Foster RG, 2002. Visual pigments and oil droplets in diurnal lizards: A comparative study of Caribbean anoles. *Journal of Experimental Biology* 205: 927–938.
- Manríquez KC, Pardo LM, Wells RJD, Alvaro TP, 2008. Crypsis *Paraxanthus barbiger* (Decapoda: Brachyura): Mechanisms against visual predators. *Journal of Crustacean Biology* 28: 473–479.
- Melin AD, Fedigan LM, Hiramatsu C, Sendall CL, Kawamura S, 2007. Effects of colour vision phenotype on insect capture by a free-ranging population of white-faced capuchins *Cebus capucinus*. *Animal Behaviour* 73: 205–214.
- Merilaita S, 2003. Visual background complexity and the evolution of camouflage. *Evolution* 57: 1248–1254.
- Middendorf GAI, Sherbrooke WC, 1992. Canid elicitation of blood squirting in a horned lizard *Phrynosoma cornutum*. *Copeia* 1992: 519–527.
- Morey SR, 1990. Microhabitat selection and predation in the Pacific treefrog *Pseudacris regilla*. *Journal of Herpetology* 24: 292–296.
- Neitz J, Geist T, Jacobs GH, 1989. Color vision of the dog. *Visual Neuroscience* 3: 119–125.
- Norris KS, Lowe CH, 1964. An analysis of background color matching in amphibians and reptiles. *Ecology* 45: 565–580.
- Ruxton GD, Speed M, Sherratt TN, 2004. *Avoiding attack: The evolutionary ecology of crypsis, warning signals and mimicry*. Oxford: Oxford University Press.
- Sargent TD, 1969. Background selections of the pale and melanic forms of the cryptic moth, *Phigalia titea* (Cramer). *Nature* 222: 585–586.

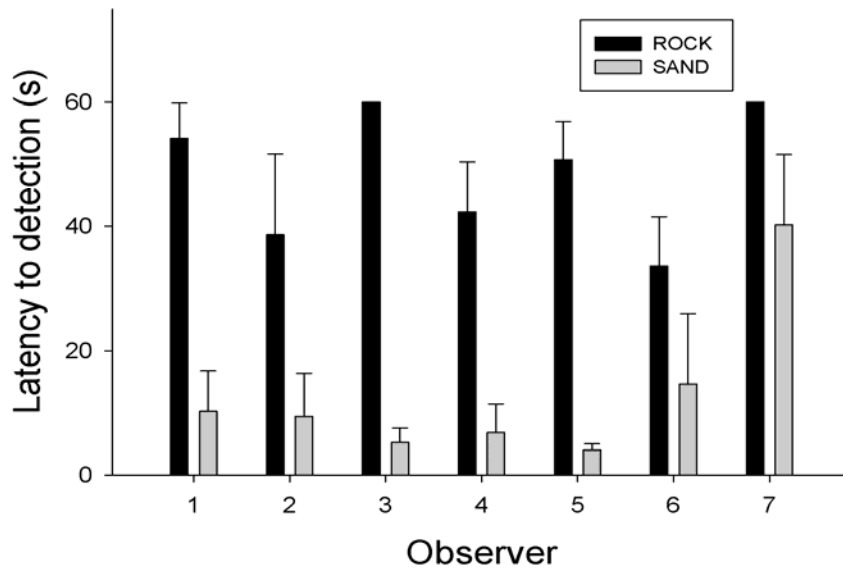
- Sherbrooke WC, 1990a. Rain-harvesting in the lizard *Phrynosoma cornutum*: Behavior and integumental morphology. *Journal of Herpetology* 24: 302–308.
- Sherbrooke WC, 1990b. Predatory behavior of captive greater roadrunners feeding on horned lizard. *Wilson Bull.* 102: 171–174.
- Sherbrooke WC, 1997. Physiological (rapid) change of color in horned lizards *Phrynosoma* of arid habitats: Hormonal regulation, effects of temperature, and role in nature. *Amphibia-Reptilia* 18: 155–175.
- Sherbrooke WC, 2003. Introduction to horned lizards of North America. Berkeley: University of California Press.
- Sherbrooke WC, 2008. Antipredator responses by Texas horned lizards to two snake taxa with different foraging and subjugation strategies. *Journal of Herpetology* 42: 145–152.
- Sherbrooke WC, Frost SK, 1989. Integumental chromatophores of a color-change, thermoregulating lizard *Phrynosoma modestum* (Iguanidae; Reptilia). *American Museum Novitates* 2943: 1–14.
- Sherbrooke WC, Middendorf GA, 2004. Responses of kit foxes *Vulpes macrotis* to antipredator blood-squirting and blood of Texas horned lizards *Phrynosoma cornutum*. *Copeia* 2004: 652–658.
- Sherbrooke WC, Montanucci RR, 1988. Stone mimicry in the round-tailed horned lizard *Phrynosoma modestum* (Sauria:Iguanidae). *Journal of Arid Environments* 14: 275–284.
- Sillman AJ, Govardovskii VI, Röhlich P, Southard JA, Loew ER, 1997. The photoreceptors and visual pigments of the garter snake *Thamnophis sirtalis*: A microspectrophotometric, scanning electron microscopic and immunocytochemical study. *Journal of Comparative Physiology A* 181: 89–101.
- Skelhorn J, Ruxton GD, 2010. Mimicking multiple models: Polyphenetic masqueraders gain additional benefits from crypsis. *Behavioral Ecology* 22: 60–65.
- Skelhorn J, Rowland HM, Speed MP, Ruxton GD, 2010a. Masquerade: Camouflage without crypsis. *Science* 327: 51.
- Skelhorn J, Rowland HM, Speed MP, De Wert L, Quinn L et al., 2010b. Size-dependent misclassification of masquerading prey. *Behavioral Ecology* 21: 1344–1348.
- Skelhorn J, Rowland HM, Speed MP, Ruxton GD, 2011. Density-dependent predation influences the evolution and behavior of masquerading prey. *Proceedings of the National Academy of Sciences* 108: 6532–6536.
- Stuart-Fox D, Whiting MJ, Mousalli A, 2006. Camouflage and colour change: Antipredator responses to bird and snake predators across multiple populations in a dwarf chameleon. *Biological Journal of the Linnean Society* 88: 437–446.
- Vetter RS, Brodie ED, Jr., 1977. Background color selection and antipredator behavior of the flying gecko *Ptychozoon kuhli*. *Herpetologica* 33: 464–467.
- Vokey JE, Burton D, 1998. Responsiveness to noradrenaline of melanophores associated with cryptic patterning in winter flounder *Pleuronectes americanus in vitro*. *Canadian Journal of Zoology* 76: 1837–1841.
- Wright SP, 1992. Adjusted p-values for simultaneous inference. *Biometrics* 48: 1005–1013.

**Table 1** Numbers of *Phrynosoma modestum* on areas lizard-sized rocks on sand, open sand or on the line between the two areas at intervals interrupted by heavy rain at 12: 00 and 12: 30 h

Time (h)	Numbers on			<i>P</i>	<i>g</i>
	Rock	Sand	Line		
0900	13	5	2	0.10	0.40
0930	18	2	0	0.0004*	0.50
1000	15	5	0	0.041	0.46
1030	18	2	0	0.0004*	0.50
1100	19	1	0	< 0.0001*	0.50
1130	18	2	0	0.0004*	0.50
0100	18	1	1	< 0.0001*	0.50
0200	12	8	0	0.50	0.00
0230	19	1	0	< 0.0001*	0.50
0300	17	3	0	0.0026*	0.50
0400	18	2	0	0.0004*	0.50

*P* values are for binomial tests. \* - significant after Bonferroni adjustment.

FIGURE LEGEND



**Fig. 1 Latency (s) to detect a *Phrynosoma cornutum* by seven human observers in their late teens and early twenties was much longer when the lizard was among small rocks than on open sand**

Ten trials were conducted for each observer, five each on rock and sand. Values are mean  $\pm$  1.0 SE.

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