Original Article

Hiding in plain sight: a study on camouflage and habitat selection in a slow-moving desert herbivore

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Camouflage via animal coloration and patterning is a broadly important antipredator strategy. Behavioral decision making is an influential facet of many camouflage strategies; fitness benefits often are not realized unless an organism selects suitable backgrounds. Controlled experimental studies of behavioral strategies in selection of backgrounds conferring camouflage, however, are rarely paired with observations of wild populations. In order to investigate how substrate composition influenced habitat preference and selection by juvenile desert tortoises (*Gopherus agassizii*), we completed a manipulative experiment in captivity and an observational study in the wild. In our captive experiment, we found that tortoises spent a greater portion of their time near rocks. We similarly found that wild tortoises preferentially placed themselves in areas with equivalent or larger-sized rocks. Additionally, juvenile tortoises were found to be less detectable on rock substrate by observers than they were on substrate-lacking rocks. We hypothesize that rocks improve juvenile tortoise camouflage and thus that tortoises select for habitat containing rock substrate, in part, due to a survival advantage conferred by such use. The desert tortoise is a threatened species, and the present study provides a model for examining the intersection between behavior and conservation, with implications for how suitable habitat is defined and measured in species conservation programs.

Key words: **animal behavior, background matching, conservation, crypsis, desert tortoise,** *Gopherus agassizii,* **masquerading.**

INTRODUCTION

A widely studied evolutionary strategy to avoid undesired detection or recognition can be broadly described as animal camouflaging (Stevens and Merilaita 2009). Two common forms of camouflage include crypsis and masquerading. Crypsis primarily relies on coloration and pattern through mechanisms such as background matching or disruptive coloration to prevent detection (Stevens and Merilaita 2009). Masquerading, on the other hand, relies on disguising the animal form as a less-interesting object in the environment, such as a stick or even scat (Stevens and Merilaita 2009; Skelhorn et al. 2010). Although similar, crypsis and masquerading are fundamentally different in that one seeks to avoid detection entirely, whereas the other seeks to avoid recognition on detection.

In the case of both crypsis and masquerading, the visual appearance of the organism conveys antipredator benefits (Schaefer and Stobbe 2006; Skelhorn et al. 2010; Whiteley et al. 2011). The efficacy of these antipredator strategies, however, requires that animals must either only occur in well-matched areas or they must actively select habitat that maximizes their camouflage potential. Camouflage-dependent organisms can select microhabitats that reduce their predation risk (Skelhorn and Ruxton 2012) and likely increase their reproductive success (Colwell et al. 2011). This habitat selection can vary further based on individual variation in color with some degree of phenotypic plasticity (Wente and Phillips 2005; Karpestam et al. 2012; Lovell et al. 2013; Fernández Campón 2014), much as some individuals can vary color patterning to better match their microhabitat (Magellan and Swartz 2013). Furthermore, evidence suggests that selection for camouflaging backgrounds can be strengthened by the presence of a predator (Wente and Phillips 2005). Selection of habitat as a function of camouflage potential may consequently represent an important

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fitness-enhancing component driving space and habitat use by organisms (Stevens and Merilaita 2009). The extent to which laboratory camouflaging behaviors reflect habitat selection in complex wild environments and vice versa, however, is poorly documented, especially with regard to antipredator behaviors in predator-naive animals.

Animals that have largely been isolated from predators, as would be expected in most captive populations, may lack or have altered antipredator behaviors relative to their wild kin (Martin 2014). In some cases, data support innate and instinctive responses by naive prey to predator cues (Sündermann et al. 2008). In other cases, experimental design can lead to theoretical development that may poorly reflect behavior in natural conditions (Powell and Banks 2004). In order to infer evolutionary consequences of camouflaging studies, clear ties between captive behavior, behavioral decision making in wild populations, and fitness gains must be documented.

The Mojave desert tortoise (*Gopherus agassizii*) presents an opportunity to increase understanding of the proximate mechanisms and evolutionary consequences of camouflage; simultaneously, they are protected by the US Endangered Species Act, suffering wide-scale habitat loss, and in need of better definitions for suitable habitat (USFWS 2011). In general, the tortoise is a slow-moving herbivore that is presumed to rely on crypsis to reduce predation risk. They have similar coloration to their natural substrate. Although avoidance of detection through camouflage is likely their primary defense against predators when young, the extent to which individuals select habitat that increases their ability to "disappear" remains unknown. Consequently, without distinguishing between crypsis and masquerading, we sought to address 2 basic questions: 1) whether captive and wild juvenile tortoises select microhabitat that should increase their camouflaging ability and 2) whether their use of habitat potentially conferred camouflage-related fitness advantages.

To address our questions, we used 3 complementary approaches. In our first study, we used a captive population of juvenile desert tortoises in a controlled experimental choice test; we predicted that juvenile tortoises would display preference for substrate that should enhance camouflage. In the second study, we conducted field surveys of wild juveniles to measure use versus availability of substrate. In the final study, we conducted a survey of juvenile tortoises placed in preferred or nonpreferred substrates to measure relative visual detectability on each substrate by observers. Additionally, we use the results to explore the application of behavioral ecology to conservation practice by considering microhabitat needs in conservation and land management programs for camouflage-dependent species. Despite attention given to the topic in a foundational volume on conservation behavior (Endler 1997), camouflage-habitat relations have played only a small role in conservation management. Desert tortoises are experiencing range-wide declines (USFWS 2011), in part attributed to artificially inflated predator levels (Esque et al. 2010). Therefore, we hope to use the results of these studies to improve understanding of consistency between captive antipredator behaviors and microhabitat selection in the wild. In turn, we explore the role that captive and laboratory-based behavioral studies can consequently play in conservation management.

METHODS

Study locations

All hatchling tortoises used in the captive portion of this study were housed at the Desert Tortoise Conservation Center (DTCC) in Las Vegas, NV. Tortoises that originated from the DTCC came from one of 2 sources: nests created by adult tortoises undergoing rehabilitation at the DTCC or via a rescue hotline that accepted desert tortoises from the Nevada public. The wild juvenile tortoises were hatched from nests created by 20 wild females and reared in pens located at Ivanpah Desert Tortoise Research Facility (IDTRF). IDTRF is located within Mojave National Preserve, CA. Juvenile tortoises were released at 2 field sites located in Ivanpah Valley inside Mojave National Preserve. There was no overlap of animals used between studies conducted at IDTRF and DTCC, with a total of 100 live juvenile tortoises used in the study. The DTCC and IDTRF are located in the northeastern portion of the Mojave Desert, within the eastern recovery unit of the Mojave desert tortoise (USFWS 2011).

Substrate selection

In experiment 1, on selection of substrate in captivity, we placed juvenile desert tortoises (42–93-mm midline carapace length [MCL]) into arenas created by one of 6 circular plastic pools (see Figure 1 for arena specifications). We filled each arena with approximately 5 cm of soil, which we divided equally into 2 parts: half bare soil with no rock cover and half soil covered with a rock layer (Figure 1). Rock sizes were variable, but typically matched or exceeded MCL of tortoises used in the experiment (≥50 but ≤90 mm; see Figure 1 for relative sizes). We fitted each arena with 2 structures made of tan shade cloth to prevent tortoises from overheating (Figure 1). We positioned arenas inside caged outdoor enclosures, which were covered with additional shade cloth. Each tortoise had a piece of flagging tape epoxied on the carapace to improve visibility. We placed a single hatchling in the center of the arena with the anterior portion facing an easterly direction, yielding 1 tortoise per trial. We added time-lapse cameras (Ltl-5210, Ltl Acorn Outdoors, WI) 200 cm above the arena to document the
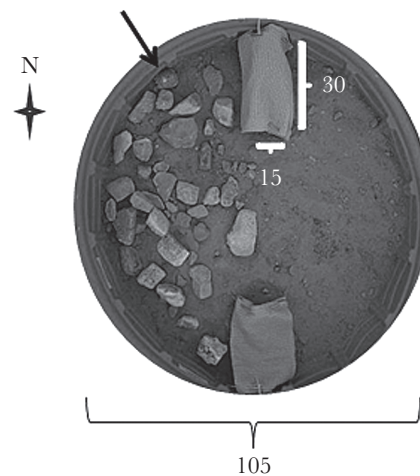
Figure 1

Substrate arenas. Children's play pools with an external dimension of 105 × 15 cm were used as arenas and evenly filled with desert soil. Soil depth was a minimum of 5 cm. Each arena was divided equally into 2 sections designated as rock substrate or bare soil along a North–South gradient. The side (east or west) that was rock substrate or bare soil varied and was randomly assigned. On the bare soil side, the substrate was left devoid of rocks. On the rock substrate portion, rocks similar in size to a juvenile desert tortoise were placed approximately 2–5 cm apart. To prevent the tortoises from overheating while occupying the arena, we installed two 30 × 15 cm long shade structures between the substrate sections at both sides of the arena. The arrow indicates the position of a juvenile tortoise.

location of the tortoise each 15 min between 6:30 and 20:00 h. To reduce cross-contamination of scent, disease, or parasites among tortoises, we replaced rocks and soil from the arena between trials and disinfected arenas and shade structures. We collected all substrate from natural washes located in the DTCC grounds.

After completion of the study, we visually reviewed images contained from a 12-h time period (46 images/tortoise). We classified each image as rock substrate, bare soil, or not visible. A tortoise was classified as not visible if the entire body was beneath the shade structure. We categorized images as rock substrate if a tortoise was visible and within one body length of a rock. The remaining images we categorized as bare soil. We calculated the proportion of time each individual spent on rock substrate from the sum of the total sightings. In cases in which cameras failed and did not document a 12-h period contained within 6:30–20:00 h, we removed the animals from the study. We originally included 64 animals in the study. Thirteen cameras failed to record in the designated time period, leaving $n = 51$. We used a 1-sample t-test, with $\mu = 0.5$ to test the hypothesis that juveniles spent significantly greater than 50% of their time on rock substrate. For all statistical tests, we used program R (R Core Team 2013) and accepted $\alpha < 0.05$.

In experiment 2, on substrate selection by wild juveniles, we outfitted 36 juvenile tortoises, between 0 and 2 years of age (41- to 64-mm MCL) with radio transmitters (BD-2, Holohil Systems Ltd., Ontario, Canada) on the fourth or fifth vertebral scute. We tracked juveniles 2–8 times per month, such that frequency increased with their activity levels, from 28 September 2012 to 30 May 2013. During their active season, we measured rock size and cover by randomly placing five 1 m² quadrats within 5 m of the animal location and at a paired location 200 m away in a random direction. This was completed each time an animal moved at least 10 m from the previous location. In each quadrat, we ocularly measured estimated ground cover by rocks (percent) and recorded presence of rocks in 3 size categories—none (<2 mm), small (2–64 mm), and large (>65 mm). Percentage of ground covered by rocks was then reclassified into 3 discrete categories—low (<10%), medium (10–49%), and high (50–100%). Rock size and cover were combined into a single substrate category (0–5; Table 1) based on their perceived camouflage potential for juvenile desert tortoises. We assigned more complex backgrounds—greater surface cover by rocks—greater values than less complex backgrounds (Dimitrova and Merilaita 2012). Similarly, rocks that were perceived to be more camouflaging—large rocks—were assigned greater values than smaller rocks. For each location, a single value for substrate category was created using the mean value of the 5 quadrats. Locations were

Table 1

Substrate was broken into 6 categories (0–5) based on the structural composition, abundance of surface rocks, and the perceived value to juvenile desert tortoises for background blending

Category	Rock size[a]	Rock cover[b]
0	None or small	Low
1	Small	Medium
2	Small	High
3	Large	Low
4	Large	Medium
5	Large	High

[a]Size categorized into small (<65 mm) or large (>65 mm) rocks.
[b]Cover categorized into low (<10%), medium (10–49%), and high (50–100%).

then categorized into "tortoise present," which was the location at which an animal was tracked to and "tortoise absent," which was the paired location 200 m away. We used a generalized linear mixed effect model with a binomial distribution to test for differential habitat use based on substrate category. We considered the habitat location as the dependent effect (tortoise present = 1; tortoise absent = 0). We treated juvenile and maternal identity as random effects in order to ensure that repeated measures of the same individual or clutch mates were not treated as independent observations. We included mean substrate category as a fixed effect predictor. Although we used mean values for our statistical models, we also present the frequencies of all substrate category encounters based on the sum values of the quadrats to help elucidate the origin of mean differences.

Predator detection

To determine whether juvenile tortoises were relatively less detectable on rock substrate than on bare soil, we taxidermied 16 juvenile tortoise carcasses (40- to 53-mm MCL) to resemble live animals. We placed tortoises along 2 paths designed to reflect the substrate conditions provided in the initial captive choice test. In this case, we measured detectability on narrowly defined substrate conditions that were determined by animal preference in experiment 1. This study should not be considered representative of all potential tortoise habitats. Each of the paths was considered a "treatment" of either bare soil or rock substrate. The bare soil path was comprised of 8 tortoises that were placed with at least 1 m between the tortoise and the closest rock in all directions. The rock substrate path had 8 tortoises that were placed on large rocks (>65 mm) at medium to high prevalence (>10% ground cover). Each path was approximately 200 m long, which was the distance required to find 8 suitable substrate patches that reflected either the bare soil or rock substrate treatment. Each path was marked by orange flagging tape, and all tortoises were placed within 5 m of the path.

Eight volunteers, who were experienced in working with this species, walked in both of the substrate paths. Each person completed 2 passes per path during which they counted the total number of tortoises observed. For our analysis, we used the sum total number of tortoises observed by each person per path, treated bare soil or rock substrate as the treatment, and selected a paired t-test due to participation of observers in both substrate trials. Consequently, bare soil detection rates should be considered a control for detection on rock substrate (McCluskey and Lalkhen 2007). To ensure a normal distribution of the errors, we used a Shapiro–Wilk test, with the assumption that $P > 0.05$ indicated normality.

RESULTS

Substrate selection

Captive juveniles spent approximately half of their time ($53 \pm 3\%$; mean ± standard error [SE]) under the cover of a shade structure. When visible, they spent the majority ($63 \pm 3\%$) of their time on rock substrate ($t_{50} = 3.7$, $P < 0.001$). For the 36 wild tortoises, we collected 250 observations (1250 quadrats), split evenly between tortoise present and tortoise absent locations. Juvenile tortoise locations correlated positively to substrate category ($\beta = 0.33$, SE = 0.16, $P = 0.04$), such that mean substrate category was larger near tortoises than at random locations (Figure 2). This difference in the means largely resulted from a decrease in substrate categories 0 and 1 and an increase in categories 3 or greater near tortoises
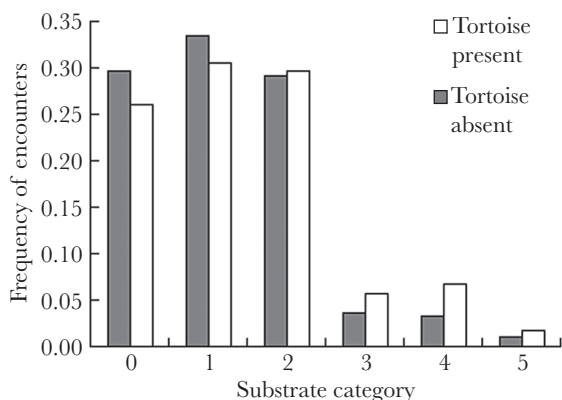
Figure 2
Substrate category based on tortoise presence or absence. In locations where tortoises were present, the mean substrate category across the 5 quadrats was significantly larger than in areas where tortoises were absent. This difference in means was due to a reduction in the frequency of encounters of category 0 and 1 substrates and a doubling in the frequency of categories 3 or greater near tortoises relative to paired locations.

(Figure 2). Specifically, 394 (63%) of the 625 tortoise absent plots possible were composed of substrate that was either bare soil (category 0) or had low cover by small rocks (categories 1). In contrast, encounters of those same substrates were reduced by 11% in the vicinity of tortoises, whereas encounters of substrate comprised of larger rocks at any cover rank doubled. Larger substrate categories (≥3), however, still made up a small proportion of total substrate encounters even near tortoises, reflecting their relative rarity in the area (Figure 2). Encounters of tortoises at category 2 substrates were approximately equal to encounters at random (182 of 625 vs. 185 of 625, respectively), suggesting animals neither sought nor avoided areas with high cover of small rocks. In sum, captive and wild tortoise appeared to seek substrates with large surface rocks.

Predator detection

On average, detection of taxidermied hatchling tortoises located in the open on all substrates was $20 \pm 6\%$. The Shapiro–Wilk test indicated a normal distribution of the errors ($W = 0.902$, $P = 0.30$) for the detectability data. Although fairly low, detection of taxidermied tortoises on bare soil ($34 \pm 8\%$) was significantly greater than on rocky substrate ($5 \pm 3\%$; $t_7 = 3.64$, $P = 0.008$). Consequently, observers had difficulty detecting juvenile tortoises overall, but detection was reduced on rock substrate relative to bare soil.

DISCUSSION

Choice tests in captive juveniles were accurate in predicting habitat preference by wild tortoises. Furthermore, their use of habitat appeared to have adaptive advantages in the form of reduced visual detection. Our results provide support for the hypothesis that camouflaging behavior by young tortoises informs habitat selection and promotes avoidance of predator detection or recognition. There are, however, a number of other environmental characteristics independent of camouflage that may have driven juvenile preference for rock substrate. For instance, rocks may have thermal properties that likely vary from that of soil. An alternative interpretation of their preference, therefore, is that microclimate on selected rock substrate is more metabolically or physiologically favorable (Huey et al. 1989) for juvenile tortoises. Use of shade cloth within and

above the experimental arenas, however, likely controlled for some thermal differences between the substrates in the captive experiment. Differences in water flow and retention among the 2 substrates may also influence the subsequent productivity of vegetation in the surrounding areas (Nobel et al. 1992). Increased water availability in soils near rock substrate may translate to increased productivity of forage. When active, tortoises may, therefore, be more likely to use rock substrate due to greater foraging opportunities. Irrespective of why, behavioral preference of tortoises in captivity was reflective of their use of habitat in the wild, suggesting that similar decision-making processes were operating in both environments. This study clearly demonstrates that captive behaviors reflect habitat selection preferences with fitness-enhancing potential. Pairing controlled experiments with quantitative observations in nature increases the robustness of inferences regarding behavioral mechanisms that affect the efficacy of camouflage.

If preference for rock substrate was driven by camouflage potential, tortoises were relying on crypsis, masquerading, or likely some combination of both. Juvenile desert tortoises have a mottled coloration that can vary on a single individual from light tan to dark brown. The effect is coloration that closely resembles desert substrate, at least from the human perspective. In general, the fairly low detectability (34%) of juveniles placed on bare soil suggests some level of cryptic coloration. That detectability of juvenile tortoises on rock substrate was much lower suggests crypsis can be enhanced through masquerading behaviors. Horned lizards (*Phrynosoma modestum*) are likewise suspected to engage in masquerading behavior by seeking similarly sized rock substrate (Cooper and Sherbrooke 2012). Behavioral adaptations that enhance environmental blending are known to occur and have been extensively studied in moths (Kang et al. 2012, 2013). Juvenile tortoise preference for larger rocks may thus support an attempt to mimic a portion of their environment readily dismissed by predators.

Other work has suggested that visual complexity of the background habitat may be an important component of avoiding detection (Kjernsmo and Merilaita 2012). For instance, lizards in more structurally complex habitat had lower probabilities of being attacked than those in less complex areas (Shepard 2007). In blue tits, *Cyanistes caeruleus*, search time for prey species increased with more geometrically complex backgrounds or prey patterns; for their prey, however, mismatching the background carried a higher cost than association with simple backgrounds (Dimitrova and Merilaita 2012). Consequently, organisms that occur in highly heterogeneous environments, such as deserts, may be less likely to rely on background complexity to avoid detection. We did not explicitly test for background complexity. Juvenile tortoises, however, appeared to prefer large rocks at low percentages of surface cover over smaller ones at high percentages of surface cover. This finding might suggest enhanced structural complexity provided by rocks was not driving their selection of rock substrate. Clear understanding of whether background complexity is a driver of habitat selection by tortoises requires choice tests between areas that vary in visual complexity rather than just focusing on rocks.

In general, behavioral decision making has clear relationships to individual fitness (Dingemanse and Reale 2005; Lind and Cresswell 2005). Thus, via individual fitness behavioral choices subsequently scale up to population-level impacts (Blumstein and Fernandez-Juricic 2010). Selection of microhabitat that promotes camouflaging by juvenile tortoises, therefore, may have population-level consequences. Such a conclusion, however, relies on 2 assumptions: that detectability correlates with actual predation and that greater

detection by humans reflects detection rates by predators. Because hatchling tortoises presumably rely on avoiding predator encounters as their primary antipredator strategy (their shells are easily punctured), the first assumption seems warranted. Archeological records suggest that desert tortoises were an important resource to early peoples of the American deserts for thousands of years and they continue to be harvested as pets (Schneider and Everson 1989; USFWS 1994). Thus, an adaptive response by tortoises to avoid detection by humans is conceivable. Additionally, research with other species suggests that sensory processes are similar enough to extrapolate detectability by humans to other predators (Cuthill et al. 2005; Fraser et al. 2007). Overall, predation is believed to be a major cause of mortality for young desert tortoises (Berry et al. 2013). Thus, we tentatively suggest that behaviorally mediated camouflage has important consequences for desert tortoise survival in early life-stages and may have substantive population-level consequences.

By largely failing to address animal camouflage, wildlife biologists may be ignoring aspects of the habitat that have important conservation implications. For example, reptiles with more variable color patterns that use a wider range of habitats are less likely to have threatened conservation status (Forsman and Aberg 2008). A possible explanation is that variable coloration confers crypsis in a wider range of habitats or less variation reduces crypsis thereby causing fitness consequences. For instance, horned lizards that are located on substrates that enhance crypsis have shorter flight initiation distances than on less camouflaged backgrounds (Cooper and Sherbrooke 2010), suggesting differential energetic costs. In situations where conservation programs make use of tools that inherently increase vulnerability of animals to predation, better selection of suitable habitats may be critical in improving program success. For example, translocation is a widely applied tool for conservation management of desert tortoises. Yet, in many cases, individuals are more vulnerable to predators following translocation due to increased movement and exposure, lack of knowledge regarding the landscape, and lack of access to refuges (Stamps and Swaisgood 2007; Swaisgood 2010). Knowledge that juvenile desert tortoises have behavioral preferences for rock substrate identifies substrate as an important variable for managers to consider when selecting suitable habitat for conservation and translocation purposes.

Camouflage lies at the interface of behavior, habitat suitability, and conservation, yet implications of camouflaging behaviors in conservation remain relatively unexplored (but see Endler 1997). More generally, traditional habitat suitability assessments largely rely on landscape-scale habitat features (Aebischer et al. 1993). The landscape scale, while highly generalizable, can fail to capture subtle, but important habitat features. Moreover, behavior often does not figure prominently in ecologically driven models of habitat selection (Lima and Zollner 1996). However, behaviorally informed exploration of habitat selection, as conducted here, may identify important habitat features that are screened out in ecologically based habitat selection models (Andersen et al. 2000). These omissions can subsequently have substantive implications for conservation management and policy. As anthropogenic changes alter the level of predation pressure on tortoises (Berry et al. 2013), camouflage strategies may prove less effective. Predation can be anticipated to have increasing impacts in the human-altered landscapes of the anthropocence through expanding, subsidized, and invasive predator populations (Jessop et al. 2012; Kristan and Berry 2003) and mesopredator release (Crooks and Soule 1999; Gompper

and Vanak 2008). Additionally, invasive plants may alter the background (Brooks 2000) in a way that exacerbates inflated predator populations, if tortoises become more conspicuous. Managers will need to realize that perceptual processes, such as those supporting camouflage, may affect the potential of habitat for supporting prey species and require different management strategies to address them. As practitioners and theoreticians strive to better integrate behavior and conservation (Berger-Tal et al. 2011), we suggest a future focus should be improving understanding of how to maintain and manage habitat for camouflage-dependent species.

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