ORIGINAL PAPER

Foraging tactics of an ambush predator: the effects of substrate attributes on prey availability and predator feeding success

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Abstract The foraging sites selected by an ambush forager can strongly affect its feeding opportunities. Foraging cane toads (*Rhinella marina*) typically select open areas, often under artificial lights that attract insects. We conducted experimental trials in the field, using rubber mats placed under lights, to explore the influence of substrate color and rugosity on prey availability (numbers, sizes, and types of insects) and toad foraging success. A mat's color (black vs. white) and rugosity (smooth vs. rough) did not influence the numbers, sizes, or kinds of insects that were attracted to it, but toads actively preferred to feed on rugose white mats (50% of prey-capture events, vs. a null of 25%). White backgrounds provided better visual contrast of the (mostly dark) insects, and manipulations of prey color in the laboratory showed that contrast was critical in toad foraging success. Insects landing on rugose backgrounds were slower to leave, again increasing capture opportunities for toads. Thus, cane toads actively select backgrounds that maximize prey-capture opportunities, a bias driven by the ways that substrate attributes influence ease of prey detection and capture rather than by absolute prey densities.

Keywords Foraging success · Prey choice · Prey selection · *Bufo marinus* · Sit-and-wait predation

Communicated by P. Bednekoff

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Introduction

For any mobile predator, a primary determinant of foraging success is the selection of sites in which to search for prey. Often, the numbers of prey and their vulnerability to the predator show strong spatial heterogeneity, such that we might expect predators to evaluate potential foraging sites carefully before choosing specific hunting locations (Adams 2000; Heiling 1999; Hopcraft et al. 2005; Inoue and Matsura 1983; Scharf and Ovadia 2006). The choice of a foraging site is especially significant in the case of a sit-and-wait (ambush) forager, because many such animals spend very long periods at a single site—and hence, their food intake over a substantial time period is determined by foraging success at that site (Eskew et al. 2009; Heinrich and Heinrich 1984; Webb and Shine 1998a,b). Optimality theory thus predicts that natural selection will have fine-tuned foraging-site choice criteria of ambush predators, such that these animals choose sites that maximize their opportunities for prey capture (Pyke 1984; Pyke et al. 1977).

What criteria might ambush predators use to select foraging sites, and why? Answers to those questions may give insights into important features of predator ecology, including dispersion patterns, feeding rates, and effects of anthropogenic habitat change on predator viability. An extensive body of natural history literature (much of it anecdotal) suggests that ambush predators of a diverse array of phylogenetic lineages utilize similar criteria in selecting foraging sites. Such predators exploit temporal and spatial heterogeneity in prey availability by lying in wait at sites where prey are (a) more frequently encountered and (b) less capable of detecting or avoiding the predator. For example, some spiders construct their webs near

artificial lights (e.g., *Larinioides sclopetarius*) or in sites well-illuminated by natural light (e.g., *Neoscona crucifera*), hence increasing insect abundance (Adams 2000; Heiling 1999). Lions (*Panthera leo*) wait in ambush beside water-holes (where prey are concentrated, and drinking impairs their vigilance: Hopcraft et al. 2005; Valeix et al. 2009). Similarly, island pit-vipers (*Gloydius shedaoensis*) lie in wait on tree branches located in places (e.g., at the edges of open areas, or near waterholes) that maximize rates of bird arrival, and facilitate prey capture by providing a clear visual and thermal background against which the prey can be rapidly detected and accurately seized (Shine and Sun 2002). A third criterion for ambush-site selection involves "costs" to the predator: for example, its exposure to the risk of predation or pathogen uptake (Heads 1985; Kotler 1997; Lima and Dill 1990; Lima and Bednekoff 1999; Sih 1980; Sih and McCarthy 2002). Despite the probable generality of such criteria for ambush-site selection, few cases have been examined in detail to identify (and experimentally test) hypotheses about causal effects of specific habitat attributes on (a) prey abundance, (b) ease of prey capture, and/or (c) rates of predator feeding success. Studies on free-ranging vertebrate predators are especially scarce. We have conducted such a study on an ambush-foraging anuran, to examine how and why substrate attributes affect foraging success by the predator.

Methods

Study area and species

Cane toads (*Rhinella marina*; allocated to *Bufo marinus* under previous nomenclatural schemes—Pramuk et al. 2008) are large (100–150 mm snout-urostyle length and 500–800 g average mass) anurans native to South and Central America and México, but introduced to many other countries for biocontrol purposes (Lever 2001). Brought to Australia in 1935, the toads have since spread over more than a million square kilometers through the tropics and subtropics (Urban et al. 2008). Dietary analyses indicate opportunistic feeding on a diverse array of invertebrates (and occasionally vertebrates), with a preference for relatively small prey (especially ants and beetles: Evans and Lampo 1996; Strüssmann et al. 1984; Zug and Zug 1979). Like many other bufonids, cane toads are central-place foragers and are often seen in high densities around street lamps, feeding on insects attracted to the lights (Zug and Zug 1979). In both their native and introduced ranges, cane toads exploit anthropogenically disturbed sites for access to food and water (Lever 2001; Zug and Zug 1979). Foraging toads typically remain motionless in a relatively open area until prey approaches close enough to be seized;

prey movement triggers feeding responses by the toad (Buxbaum-Conradi and Ewert 1999). We gathered data on toad foraging behavior at two sites on the Adelaide River floodplain in the wet–dry tropics of the Northern Territory: Middle Point Village (12°42′43.31″S, 131°18′52.28″E; four sampling locations used) and Leaning Tree Lagoon (12°42′43.32″, 131°25′10.56″E; five sampling locations used) 54 and 69 km southeast of Darwin, respectively. The village provides artificial light sources that attract insects at night, as well as pools of water. In contrast, the lagoon is a natural waterbody without buildings or lights, and is bordered by savanna woodland. Toads are abundant in both sites.

Field trials

Our experiments investigated the roles of two attributes of the substrate (color and rugosity) on toad behavior and foraging success and on prey availability to toads. We selected color and rugosity for study because they comprise the two most obvious axes of variation for open substrates, and both vary even over small spatial scales both in natural environments and in urban areas. Thus, foraging toads often will have the opportunity to select specific substrate colors or rugosities when moving to a foraging site.

To detect any causal effects of substrate attributes on insects and toads, we need experimental studies that clearly separate the effect of those attributes from other characteristics that are linked to them under natural conditions. For example, a substrate may be dark-colored because it is wet, and thus, may attract insects or toads for hydric reasons rather than color per se. Similarly, a dark substrate exposed to sunlight may retain heat into the night (the foraging period for adult cane toads: Zug and Zug 1979), and thus, affect insects or toads for thermal reasons. On the other hand, substrate rugosity may be correlated with other variables such as water availability; rugose surfaces retain water for longer periods than smooth ones and thus can be chosen for hydric reasons. Additionally, the relative frequency of rough versus smooth substrates differs between undisturbed and disturbed areas; for example, concrete floors under houses are smoother than almost any natural substrate on which we have seen feeding toads. To eliminate any such correlative effects, we manipulated substrate attributes by using four 750 mm squares of heavy-duty rubber sheeting (3.6-mm thick, as used for floor mats in automobiles) that differed in color (black vs. white) and texture (rough vs. smooth; the "rough" mats had 324 raised areas per 100 cm^2). We ran trials on 11 different nights (using both locations on each of these nights, with the order of testing alternating between locations), and used two replicate mats of each type for our experiments.

Each trial consisted of placing four mats (one of each type, i.e., white rough; white smooth; black rough; black

smooth) on the ground to form a large (1.5×1.5 m) square with their inner edges in contact. To attract insects (and thus toads), we placed one 250-mm fluorescent tube bulb (12 V, 8 W) on a tripod 1 m above the center of the larger square. The position of the four substrate types was randomized between trials. The observer sat 2.5 m from the apparatus and recorded the following variables for each substrate type:

(1) Toad feeding rates (number of predation attempts over a 5-min period as inferred from feeding movements; we could not always detect whether or not the attempt was successful). A total of 49 toads were observed during different nights. Each observation began as soon as the toad arrived on one of the mats. When more than one toad occurred on the mats at the same time, we chose a focal individual and ignored the others. To avoid taking data on the same individual more than once, each toad was collected at the end of the observation period and kept in a moist bag until the nights' trials had concluded. Given the high vagility (Alford et al. 2009) and high abundance of toads at the sites we worked, inadvertent resampling of the same toads on different nights was highly unlikely.

(2) Numbers, sizes, and types of insects attracted over a 30-min period (collected on sticky tape affixed to each mat and counted, measured, and identified later from two 200×80 mm sections of the tape; all insects were scored as either black, white, or brown). This method may underestimate the numbers of insects more capable of escaping (e.g., larger individuals), but this bias is likely to be minor. Large insects were rarely attracted to the lights, and we saw few insects escape after they touched the tape.

(3) Retention time of a random subsample of insects on each substrate type (time elapsed from arriving to leaving, based on direct observation with no toads present).

Data on each of these three variables were obtained from trials conducted on different nights from July to October during the dry season in 2009. Temperature during these trials ranged from 21.8°C (61% humidity) to 27.3°C (58% humidity).

Laboratory trials

To evaluate the possibility that rough substrates enhanced prey-capture rates because they provided more secure footing for the toads, we quantified effects of mat rugosity on toad locomotor performance (distance jumped). If smooth mats do not provide secure footing, more rugose mats should enhance jumping distances. We captured 18 toads, and tested them the following night by placing each

toad on a mat then touching its urostyle to stimulate a jump. We recorded the distance covered, then tested the toad on the other type of mat (half the toads were first tested on rough mats, half were first tested on smooth mats).

Because it was logistically impossible to score attributes of insects seized vs. ignored on different substrate types by toads in the field, we examined potential effects of substrate color on prey detection in the laboratory. Toads were collected from our field sites and kept without feeding for 48 h (to standardize hunger levels) before trials. Each toad was then individually tested in a 60×36 cm enclosure at the toad's usual feeding time (2000–2300 hours). Each enclosure had either a white or dark smooth substrate (the same mats as used in the field trials), and contained ten crickets (five white and five black in color). To manipulate color, the crickets were dusted in a mixture of chalk and calcium powder (rendering them white) or charcoal powder (rendering them black). The powder did not affect cricket locomotion. The same illumination source (fluorescent tube bulb 250 mm, 12 V, 8 W) used during the field trials was placed 1 m above the arena. We scored the color of the first prey item seized by the toad.

Statistical analysis

Data were checked for normality and variance heterogeneity, and satisfied these assumptions except for percentage data (which had to be ln[1+X] transformed to meet the assumptions). We examined the effect of substrate traits on a toad's feeding rate (total number of prey attacked) by including mat types (i.e., different substrate colors and rugosities) as the repeated measure in an ANOVA. Effect of substrate traits on insect arrival rates, body sizes, colors, taxonomic composition, and the duration of insect availability on the mats were also tested using two-factor ANOVAs with substrate color and rugosity as the factors. Jumping distances on smooth versus rugose mats were compared with a paired t test. Toad prey selection as a function of color contrast with the substrate was analyzed by a logistic regression with "prey color chosen" as the dependent variable and substrate color as the factor. Analyses were made in JMP 5.0.1 software (SAS 2002).

Results

A total of 5,166 insects were scored. The insect samples collected from our two study sites differed significantly in mean values for size and color, and in taxonomic composition (Table 1). However, patterns with respect to substrate color were similar at the two sites, and statistical analyses revealed no significant interactions between site and substrate attributes for any variable that we examined (all $P > 0.05$).

Table 1 A comparison of the attributes of insects attracted to our experimental substrates at two sites, based on field trials conducted using artificial light

Variable	Middle Point Village	Leaning Tree Lagoon	Comparison among locations
	Mean (SE)	Mean (SE)	
Number of insects	37.4 (7.1)	74.4 (11.6)	$F_{1,86}=6.68$, $P=0.01$
Mean body size (mm)	4.45 (0.29)	3.12 (0.13)	$F_{1,86}=19.41$, $P<0.001$
Taxonomy –			
% Hemipterans	57.4 (5.4)	30.1 (3.4)	$F_{1,82}=17.61$, $P<0.001$
% Coleopterans	7.5 (2.9)	43.5 (3.2)	$F_{1,82}=82.68$, $P<0.001$
% Ephemeropterans	15.8 (4.3)	1.7 (0.5)	$F_{1,82}=15.68$, $P<0.001$
Color			
% White	2.2 (0.8)	4.1 (0.8)	$F_{1,74}=2.39$, $P=0.13$
% Black	49.9 (3.6)	37.3 (2.3)	$F_{1,74}=9.25$, $P<0.001$
% Brown	23.2 (3.8)	38.7 (2.4)	$F_{1,74}=12.47$, $P<0.001$

Forty trials were conducted at each site. The final column shows the result of a one-factor ANOVA comparing these attributes between the two sites. Data on percentage composition were ln(1+X) transformed prior to statistical analysis, but untransformed mean values are shown to aid interpretation

Hence, for simplicity of presentation, we combined samples from the two sites in the analysis below; analyses incorporating site as a factor yield identical conclusions.

Effect of substrate traits on toad feeding rates

The number of predation attempts by toads was affected by substrate color and substrate rugosity (Fig. 1a; repeated measures ANOVA, $F_{3,144}=8.63$, $P<0.0001$). More than twice as many attempts were made to capture prey items from the rough white surface than from any other substrate type.

Effect of substrate traits on insect arrival rates, body sizes, colors, and taxonomic composition

The color and rugosity of the rubber mat did not have a significant influence on any of the insect characteristics that we scored (Table 1). Apart from a non-significant trend for white mats to attract more insects than black mats, all of the mean values for all insect-related variables were very similar among the four mat types. Thus, the color and rugosity of a mat did not affect the numbers (Fig. 1b), mean body sizes (Fig. 1c), colors (Fig. 2) or taxonomic composition (Fig. 3) of the insects alighting on that mat (see Table 2 for statistical analyses).

Contrast between insect color and substrate color

Although the color and rugosity of a mat did not significantly affect which colors of insects alighted upon it (see above), there were many more dark-colored insects than light-colored ones overall (57% black, 39% brown, 4% white; see Fig. 2). Thus, the white mats provided a background with greater visual contrast for most insects, than did the black mats.

Duration of insect availability after arrival

The interval between an insect alighting on a mat and leaving the mat (i.e., the time that the insect was potentially available to a foraging toad) was affected by substrate rugosity ($F_{1,948}=8.68$, $P<0.004$) but not color ($F_{1,948}=3.14$, $P=0.08$; interaction $F_{1,948}=1.76$, $P=0.19$). Insects alighting on rugose mats remained on the mat surface longer than on smooth mats (Fig. 1d).
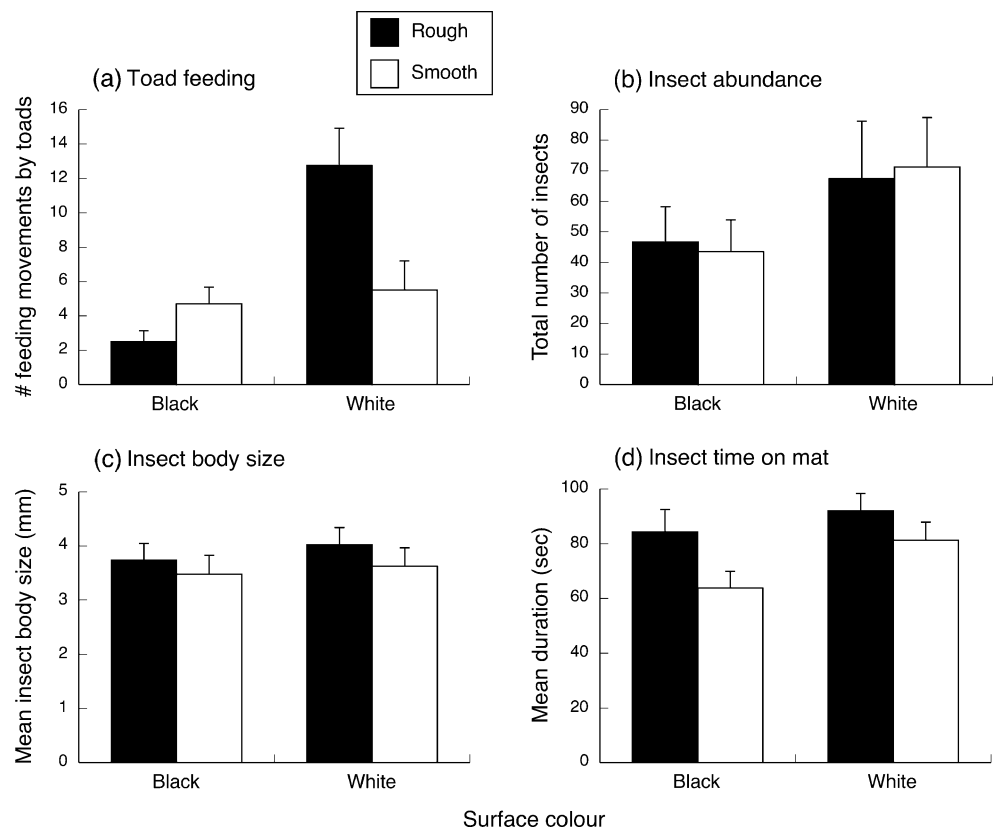
Jumping distances of toads as a function of substrate rugosity

Jumping distances were not significantly correlated with toad body size (means 23.8 and 23.0 cm, respectively; $n=18$, paired $t=0.33$, $P=0.74$), nor did they differ significantly between rugose and smooth mats (rugose mat, $n=18$, $r=-0.04$, $P=0.88$; smooth mat, $n=18$, $r=-0.23$, $P=0.35$).

Prey selection by toads as a function of color contrast with the substrate

In laboratory trials, toads were more likely to seize a dark-colored than light-colored prey item overall (72% vs. 28%, $N=95$; against a null hypothesis of 50%, $\chi^2=17.69$, $df=1$, $P<0.001$). However, the prey's visual contrast against the background affected predation, with greater contrast in-

Fig. 1 Influence of substrate (rubber mat) color and rugosity on toad feeding rates and prey availability based on trials conducted in the field. Panels show: **a** number of feeding movements by toads per 5 min; **b** number of insects alighting per 30 min; **c** mean body sizes of insects alighting over a 30-min period; and **d** duration of time that individual prey items potentially were available to foraging toads (i.e., interval between arrival and departure of the insect). *Error bars* show one standard error

Discussion

The interaction between two major attributes of the substrate (color and rugosity) strongly influenced feeding rates of free-ranging cane toads in our field experiments (Fig. 1a). Plausibly, that bias might reflect either insect availability, or ease of prey capture. In our study system, substrate attributes did not affect the numbers, sizes, colors or types of insects alighting (Figs. 1b,c, 2 and 3), suggesting that substrate type affects toad feeding rates by facilitating prey capture rather than by attracting more or different prey. In keeping with this interpretation, substrate rugosity made insects easier to catch (probably because they remained longer on rugose surfaces before leaving. An alternative hypothesis (that toads obtained a firmer foothold on rougher mats) was not supported by our laboratory trials. White backgrounds provided greater visual contrast to most prey items. In the laboratory, visual contrast between the prey and background enhanced feeding rates of toads (Fig. 4). Contrast of prey against the background is an important cue for prey recognition by toads (Ewert and Siefert 1974; Ewert and Kehl 1978), and has been manipulated to affect toad foraging responses in previous

creasing predation rates (likelihood ratio $\chi^2 = 3.99$, $df = 1$, $P < 0.05$; see Fig. 4).

studies (Aho et al. 1993; Robins and Rogers 2004). In total, our data show that substrate attributes can influence the feeding rates achievable by an ambush predator, and clarify the proximate mechanisms that generate that link between habitat attributes and predator foraging success.

Specific features of our study system minimized sources of variation that are important in other systems. First, cane toads are highly toxic and have few predators in their introduced range (Lever 2001; Shine 2010). That relative invulnerability may reduce the importance of predation risk in the selection of ambush-foraging sites; cane toads may simply go where feeding opportunities are greatest, without as much regard to risk-reducing factors (such as proximity to cover) as for some other ambush foragers. For example, many lizards, birds, and mammals dart out to seize prey from places of concealment (crevices, burrows, shrub, vegetation), such that proximity to cover may be more important than substrate attributes in determining ambush-site selection (Cooper et al. 1999; Huey and Pianka 1981; Kotler et al. 1991; Megan and Fernández-Juricic 2009; Searle et al. 2008). Thus, although cane toads may evaluate predation risk when selecting foraging sites, we doubt that predation risk is a major influence on foraging-site selection. Second, cane toads do not rely on camouflage to allow close approach by their prey, or to reduce their chances of discovery by larger predators. Although nocturnal insects sometimes detect and avoid oncoming toads (E.
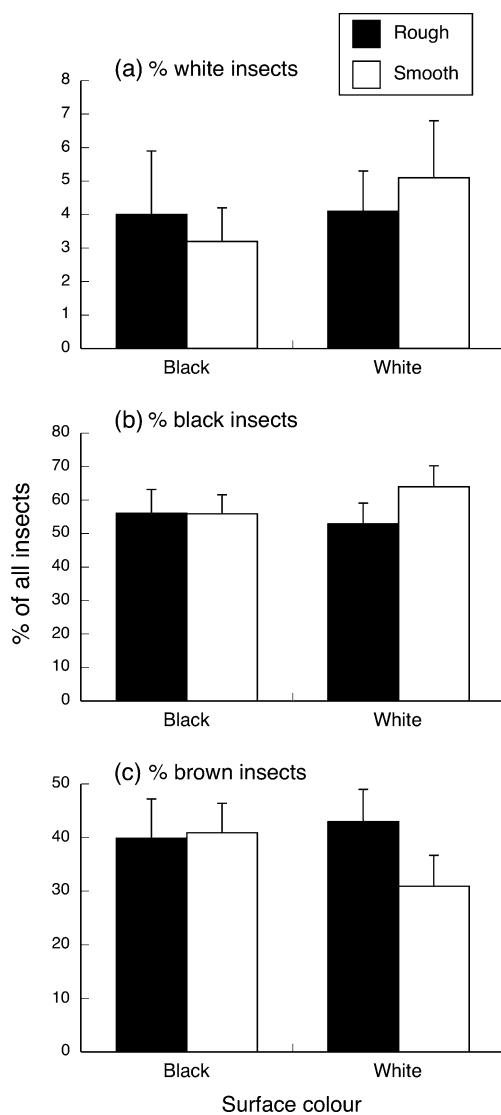
Fig. 2 Influence of substrate (rubber mat) color and rugosity on the proportion of white, black, and brown insects alighting over a 30-min period during field trials. The insects were attracted by artificial lights. *Error bars* show one standard error

Fig. 3 Influence of substrate (rubber mat) color and rugosity on the taxonomic composition of insects alighting on those mats over a 30-min period during field trials. *Error bars* show one standard error

González-Bernal pers. obs.), most insects attracted to artificial light likely are unable to accurately assess their surroundings before being seized. In contrast, camouflage against the background may be a critical element of ambush-site selection for many predatory species (e.g., Li et al. 2003; Théry and Casas 2002). Third, substrate attributes had minimal or no effect on the availability of prey in our study system; flying insects were attracted to the artificial lights, and their eventual landing sites apparently were determined by chance rather than by substrate characteristics. In many predator–prey systems, substrate attributes will strongly affect prey availability, because alternative substrates differ in the resources important to those prey animals (e.g., Eskew et al. 2009; Hopcraft et al. 2005; Webster and Hart 2004).
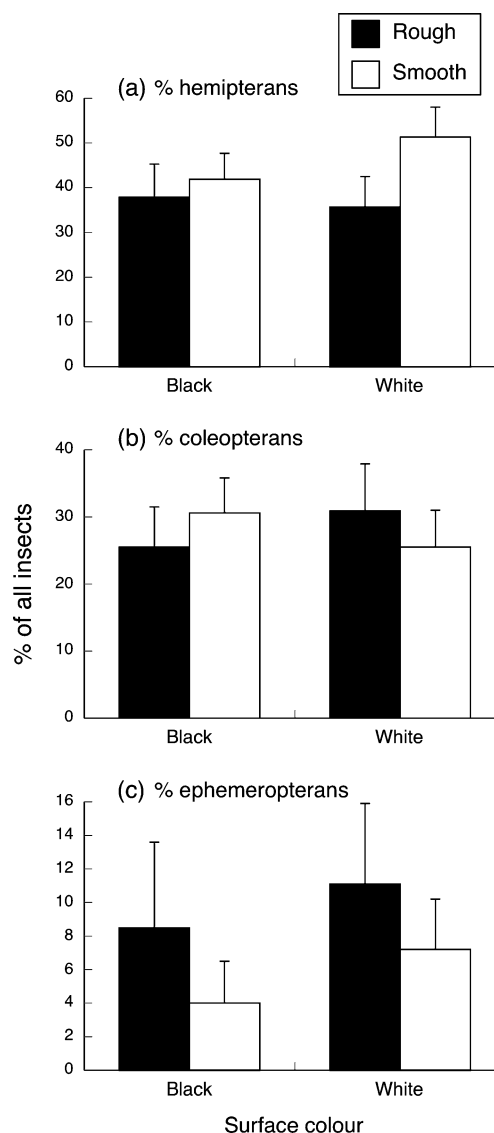
The lack of these confounding effects is a major advantage of our study system, because it allows us to focus clearly on a single phase of the predator–prey interaction that affects predator foraging success. That is, given that a prey item is available within range of the predator's feeding strike, what attributes of the substrate affect predator feeding rates? Our data identify two such causal effects. First, background color (and thus, the degree of visual contrast between prey and substrate) affects the ease of prey detection. Second, substrate rugosity facilitates prey capture, apparently by increasing the duration of the prey item's proximity (and thus, vulnerability) to the predator. A rougher substrate also may provide a firmer footing for the predator as it launches an attack; but our laboratory trials do not support this idea, and our

Table 2 Effects of substrate color and rugosity on attributes of insects alighting on that surface, based on field trials under artificial light

The table gives results of statistical analyses (two-factor ANOVAs) of the effects of substrate rugosity and color on numbers, sizes, colors, and taxonomic identity of insects arriving during a 30-min observation period. * = interaction

Variable	Substrate rugosity	Substrate color	Rugosity*color
Number of insects	$F_{1,84}=0.001, P=0.99$	$F_{1,84}=2.70, P=0.10$	$F_{1,84}=0.06, P=0.81$
Mean body size (mm)	$F_{1,84}=0.44, P=0.51$	$F_{1,84}=0.97, P=0.33$	$F_{1,84}=0.04, P=0.83$
Taxonomy			
% Hemipterans	$F_{1,80}=0.29, P=0.59$	$F_{1,80}=2.13, P=0.15$	$F_{1,80}=0.75, P=0.39$
% Coleopterans	$F_{1,80}=0.001, P=0.98$	$F_{1,80}=0.001, P=0.98$	$F_{1,80}=0.75, P=0.39$
% Ephemeropterans	$F_{1,80}=0.53, P=0.47$	$F_{1,80}=1.10, P=0.30$	$F_{1,80}=0.006, P=0.94$
Color			
% White	$F_{1,80}=0.42, P=0.52$	$F_{1,80}=0.01, P=0.94$	$F_{1,80}=0.36, P=0.55$
% Black	$F_{1,80}=0.16, P=0.69$	$F_{1,80}=75, P=0.39$	$F_{1,80}=0.79, P=0.38$
% Brown	$F_{1,80}=0.32, P=0.58$	$F_{1,80}=82, P=0.37$	$F_{1,80}=1.11, P=0.29$

observations of feeding toads suggest that both types of mats provided secure footing. Toads rarely took more than one or two small steps prior to seizing an item, making substrate rugosity relatively unimportant in this respect. These general principles may be of widespread significance for ambush-site selection in many species. Spatial and temporal variation in opportunities for prey detection and prey vulnerability may be at least as great as variation in prey abundance; and if so, predator feeding rates are maximized by selecting foraging sites where prey are most easily detected and captured, rather than where they are most common (Adams 2000; Li et al. 2003). The two factors interact in complex ways. For example, the stream-drifting invertebrates consumed by juvenile salmon (*Salmo salar*) are more abundant in fast currents. Hence, the best places for salmon foraging are fast currents if light levels enable the predator to accurately detect and seize the prey item before it is carried downstream; but, when light dims and prey contrast against the background is reduced, salmon switch

from such sites to slower currents, where prey abundance is lower but prey can be detected and seized more accurately (Metcalfe et al. 1997).

It is difficult to compare our results with those of previous studies. Few previous experimental studies of free-ranging vertebrate predators have measured the kinds of variables that we have quantified, because studies of this type would face major logistic hurdles for most species. The abundance of cane toads, and their willingness to gather under artificial lights to feed, greatly facilitated our work. The situation mimicked by our experimental protocols is not "natural", in that we used artificial lights (and substrates), but the cane toad's success as a colonizing species depends to a large degree on its ability to exploit such opportunities; these toads specialize on using disturbed habitats (Lever 2001; Zug and Zug 1979). Thus, although the use of illuminated feeding stations is unnatural, it is a consistent and important aspect of the ecology of this invasive species. By conducting most of our studies in the field, on free-ranging animals, we avoided the need to extrapolate from even more artificial conditions in the laboratory. Similar experimental protocols likely would work also for small vertebrate predators of other lineages (e.g., fishes, lizards, passerine birds, rodents) as well as invertebrates (e.g., ants, dragonfly larvae) that respond to similar cues of contrast or movement. Such studies would enable us to make direct comparisons about the significance of substrate attributes for ambush-site selection in a range of predator species. One aspect of particular interest involves the parallel exploitation of artificial lights as a means of concentrating insect prey by many insectivores, by native taxa (e.g., spiders; Heiling 1999), as well as invasive species, such as cane toads (present study) and house geckos (*Hemidactylus frenatus*: E. L. González-Bernal pers. obs.). Thus, photopollution by human activities (Longcore and Rich 2004) can provide a foraging habitat superior to any available under natural conditions, with the combination of high light levels and pale-colored homo-
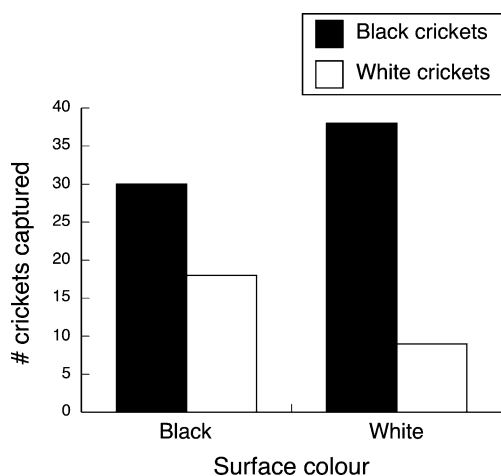

Fig. 4 Effect of visual contrast between prey and substrate colors on predation rates by cane toads in the laboratory. Toads took more dark-colored crickets overall, but visual contrast also increased cricket vulnerability

geneous substrates greatly facilitating both prey availability and ease of prey capture.

Importantly, our protocol provides experimental tests of causal effects, as well as documenting correlational patterns. Given the multiple evolutionary origins of ambush-foraging across a wide range of phylogenetic lineages, including both vertebrates and invertebrates (Adams 2000; Eskew et al. 2009; Heiling 1999; Heinrich and Heinrich 1984; Hopcraft et al. 2005; Inoue and Matsura 1983; Li et al. 2003; Megan and Fernández-Juricic 2009; Metcalfe et al. 1997; Scharf and Ovadia 2006; Shafir and Roughgarden 1998; Shine and Sun 2002), there are abundant opportunities for comparative analysis of the role of substrate attributes in predator foraging success.

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