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The predation cost of female resistance

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Mating costs to females can result in female reluctance to mate and the evolution of seemingly costly rejection strategies. The costs of mating have been widely studied; however, the costs of resistance have rarely been quantified. In the Lake Eyre dragon, *Ctenophorus maculosus*, gravid females flip over onto their backs to prevent superfluous matings. In doing so, they compromise their camouflage as females have bright orange ventral coloration during the breeding season. Visual models confirmed that resisting females are much more conspicuous to birds, their primary predator, than unresisting females. We assessed the predation risk of female resistance via a large-scale field experiment using model female lizards. Although the flipped over, orange models were more conspicuous to visual predators, they were attacked significantly less than cryptic models. It appears that predators avoid the bright females, possibly because they do not recognize orange individuals as food or avoid rare, conspicuously colored prey. Thus, conspicuous female rejection displays may be maintained in part by apostatic selection, in which predators form a search image for and preferentially attack more common prey types. *Key words:* apostatic selection, female resistance, lizard, predation risk, sexual conflict, visual ecology. *[Behav Ecol 21:861–867 (2010)]*

Sexual conflict over mating rates can generate a coevolutionary process between the sexes where females evolve behavioral or morphological adaptations to resist male courtship and copulation attempts, and in turn males develop traits to circumvent this resistance (Chapman et al. 2003). In many species, males have evolved coercive mating strategies to increase their reproductive output. This strategy is most likely to be employed by males that do not invest in their offspring and have a short life expectancy or lack exclusive access to females (Clutton-Brock and Parker 1995). Mating, particularly coercive mating, can be costly to females, decreasing the probability of female survival and reproduction (e.g., Sakurai and Kasuya 2007). Costs of mating have been widely studied and include increased mortality (Le Boeuf and Mesnick 1990; Blanckenhorn et al. 2002; Ronn et al. 2006), energetic costs (Watson et al. 1998), and increased predation risk (Arnqvist 1989). When males are capable of overpowering females and forcing copulation, there are also significant indirect costs, most notably the curtailment of female mate choice. As a result, females may mate with lower quality males that invest less in their offspring, leading to the production of inferior offspring (Cotar et al. 2008).

Because forced copulations are generally costly to females, in many species, females have evolved counteradaptations to mitigate these costs (Arnqvist and Rowe 2002). Specifically, females of many species have evolved behavioral resistance strategies or morphological adaptations to make it difficult for males to force copulation (Arnqvist and Rowe 1995; Chapman et al. 2003). In species where resistance is observed, females are often successful in preventing forced copulations or employ postcopulatory retaliation by ejecting unwanted sperm (Helfenstein et al. 2003) or controlling which sperm fertilize their eggs (Clutton-Brock and Parker 1995). Consequently, even when mating is coercive, females may retain some control over the paternity of their offspring. However, resistance strategies themselves are likely to be costly, so there will be a tradeoff between the costs associated with mating and costs of resistance. Female resistance strategies are expected to evolve when the direct and indirect benefits from preventing mating exceed the costs associated with resistance (Muhlhauser and Blanckenhorn 2002). Although the costs of mating are well studied, the costs of resistance have rarely been quantified. To understand the evolution of female resistance, however, we need to quantify both the costs of mating and of resistance.

The Australian Lake Eyre dragon lizard, *Ctenophorus maculosus*, provides a remarkable example of female resistance in a vertebrate. Males attempt to force copulation with unreceptive females and persistently harass both receptive and unreceptive females by chasing and biting them in attempts to gain a mating grasp (Olsson 1995a). Males may gain paternity by forcing copulation if females are able to store sperm, as in other small agamid lizards (Uller and Olsson 2006; Olsson et al. 2009). During copulation and forced copulation attempts, males force females to the ground and bite them on the nape of the neck, which can result in injury or even death of the female (Olsson 1995a). To mitigate the costs of mating, *C. maculosus* females resist males with 3 rejection behaviors (Olsson 1995a). Females may initially attempt to flee from the courting male or perform a threat display where they laterally compress their body, lower their gular fold and arch their back while moving in a rocking motion sometimes accompanied by a stiffened walk and tail flicks. When initial resistance fails, females perform an unusual rejection display where they flip over onto their back, exposing bright orange ventral coloration. Although female rejection behaviors are common in Iguanian lizards (families Agamidae, Chamaeleonidae and Iguanidae; (Cooper and Greenberg 1992) the flipping over behavior has been documented only in Lake Eyre dragons lizards and a species of insect (Arnqvist 1992). This behavior prevents forced male intromission as males are unable to gain a mating grasp or adopt a mating position (biting the female's neck, aligning his body on top of and parallel with hers, and wrapping his tail around the base of hers). Unusually, in *C. maculosus*, only females develop conspicuous breeding coloration, whereas males remain relatively cryptic, although in a number of other lizard species, females develop breeding coloration that differs from that in males (Cooper

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and Greenberg 1992). Female *C. maculosus* develop bright orange ventrolateral coloration on the throat and abdomen prior to becoming receptive and maintain this coloration throughout the reproductive cycle until laying, after which the orange coloration fades (Mitchell 1973; Chan et al. 2009; Jessop et al. 2009). The ventral location of female breeding coloration allows them to maintain their crypticity, however, when performing the flip-over rejection, crypsis is compromised. As *C. maculosus* is restricted to the dry salt lakes of Australia's arid southern interior, such behavior seems costly for an animal that inhabits such a featureless and exposed environment. A flipped-over female should be highly conspicuous against the uniform salt crust of Lake Eyre. Consequently, the flip-over rejection of *C. maculosus* has been widely cited as an example of sexual conflict leading to costly female resistance (e.g., Eberhard 2002; Cunningham 2003; Shine et al. 2003).

Although female resistance in *C. maculosus* has been assumed to increase the risk of predation, until now, the direct predation costs have not been investigated. In this study, we assessed the predation cost of increased conspicuousness associated with female resistance. First, we evaluated the conspicuousness of *C. maculosus* females as perceived by an avian predator. We then assessed the predation risk of flipped over, resisting females relative to that of cryptic, nonresisting females with a large-scale field experiment using model lizards. This system is particularly amenable to using static models to assess predation risk as the most common antipredator behavior employed by *C. maculosus* is to crouch down and remain motionless (Mitchell 1973) and the flip-over rejection of *C. maculosus* involves minimal movement. Flipping over takes less than a second and the female remains motionless for up to a minute while flipped over. We therefore use this approach to test the hypothesis that flipped over, resisting females are more conspicuous to visual predators and therefore more likely to be attacked.

MATERIALS AND METHODS

Study system and study site

The Lake Eyre dragon, *C. maculosus*, is a sexually dimorphic agamid lizard (mean snout–vent length (SVL) of 70 and 60 mm for males and females, respectively) endemic to the 3 largest salt pans of arid inner South Australia (Mitchell 1973). The main predators of *C. maculosus* are hawks and other birds of prey although they are also sometimes preyed on by varanid lizards (*Varanus gouldii*), which make short forays onto the lake surface from the shore dunes (Mitchell 1973).

The study was conducted at Lake Eyre, South Australia (28.95–29.05°S, 137.65–137.76°E) between 17th September and 4th October 2008. Six of the study sites were located on the Lake Eyre salt pan and one within 20 km of Lake Eyre at the Muloorina Station bore hole (Supplementary Figure S1), which we included in order to compare predation levels on Lake Eyre with those in the adjacent vegetated sand dunes.

Model lizards

We made 200 *C. maculosus* models by modifying plastic animal replicas (Figure 1). We used replica tuatara (Science and Nature's Pty Ltd), which were a suitable size (ca. 6 cm SVL) and shape to represent female lizards. Replicas were trimmed (spinal crest removed), painted, and coated in plasticine to mimic the coloration and shape of females during the breeding season. We matched paints and plasticines as closely as possible to the color of the lizards by measuring and comparing their spectral reflectance (see below and Figure 2). Reptile models have been successfully used to investigate predation by visual predators (Brodie 1993; Castilla and Labra 1998; Stuart-Fox et al. 2003; Husak et al. 2006). The models were realistic enough that captive males displayed to them with head-bobs.

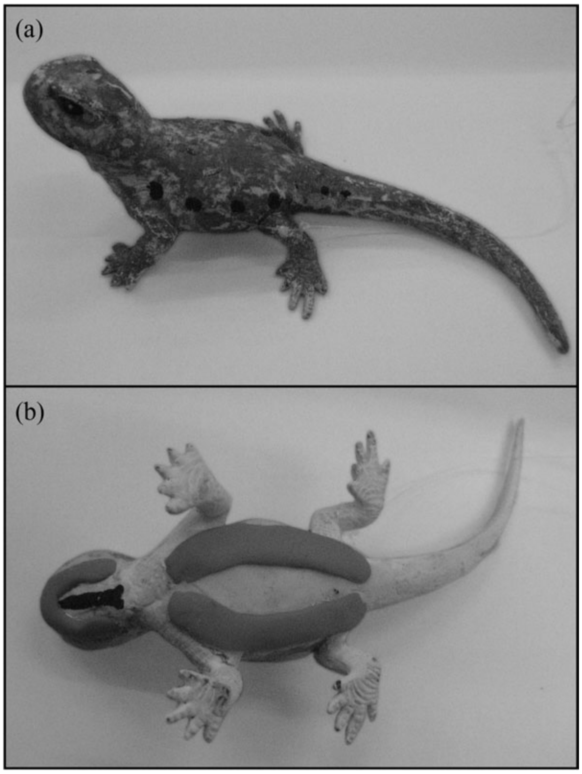

Figure 1
Ctenophorus maculosus model types: (a) female in the normal upright posture (cryptic) and (b) female flipped over in the rejection posture (orange).

Spectrophotometry

We measured spectral reflectance of paints and plasticines used to construct models and 21 wild-caught *C. maculosus* females, which had been brought into captivity. We used an Ocean Optics USB2000+ spectrometer connected to a laptop computer running Ocean Optics SpectraSuite software and a Pulsed Xenon lamp (PX-2). Measurements were taken at a 30 degree angle to the surface using a custom made probe and expressed relative to a WS-1-SL diffuse white reflectance standard. We took measurements of the brown central back, head and flanks, white belly, black spots, and orange ventral coloration of females. We took 3–5 measurements for each body region and used the mean as the representative spectrum.

To measure background spectra, we collected samples of crust and sand from the field sites at Lake Eyre, the natural environment of *C. maculosus.* We also collected and measured spectral reflectance of the background (sand, sticks, and leaves) at the Muloorina Station borehole. We took multiple measurements for each type of background and used the median measurement of each as background reflectance.

Visual modeling

To calculate a predator's ability to discriminate *C. maculosus* (real and model) from each of the 6 backgrounds, we applied the model of Vorobyev and Osorio (1998), which estimates

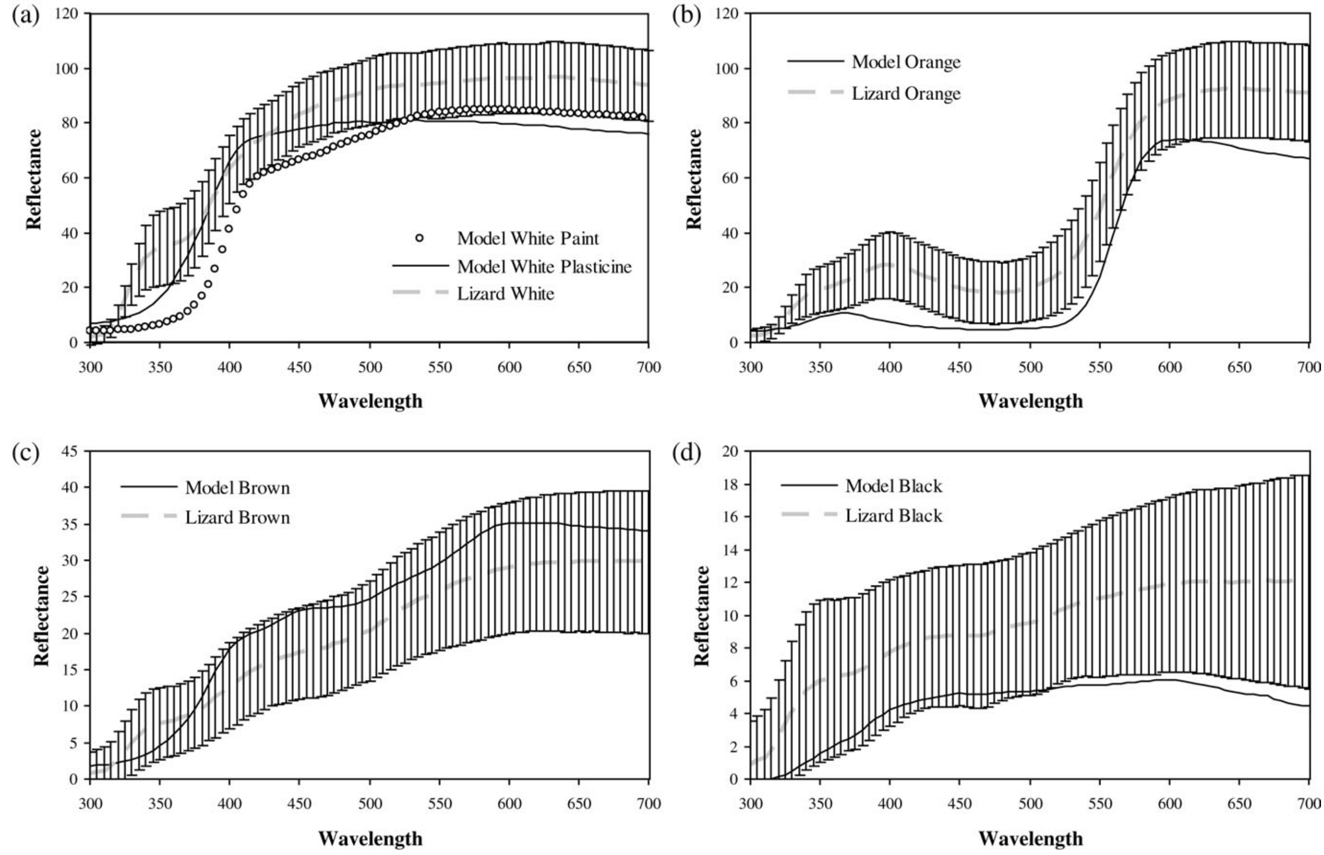

Figure 2
Reflectance spectra of *Ctenophorus maculosus* females for (a) white ventral coloration, (b) orange ventral coloration, (c) brown dorsal coloration, and (d) black spots compared with reflectance spectra of corresponding lizard model materials. Data are mean ± standard deviation of reflectance measurements from 21, 9, 20, and 17 lizards, respectively.

the discriminability of 2 colors in units of just noticeable differences. For analysis, all spectral data (lizards and backgrounds) were averaged over each 5-nm interval, in the range of 300–700 nm, the approximate visual spectrum of birds (Vorobyev et al. 1998) and most diurnal lizards (Loew et al. 2002). We applied model calculations detailed in Siddiqi et al. (2004), Stuart-Fox et al. (2003), and Supplementary Material.

The model requires data on the spectral sensitivities of the receiver (in this case birds). All birds studied to date fall in to one of 2 highly conserved categories of visual systems, ultraviolet sensitive (UVS) with a UVS cone peak sensitivity of around 360 nm and violet sensitive (VS) with a VS cone peak sensitivity of around 410 nm (Hart and Hunt 2007). Raptors, which are the most common avian predators of *C. maculosus* (Mitchell 1973), have a VS visual system, whereas corvids, which are also potential predators, have a UVS visual system (Hart and Hunt 2007). Therefore, we used average photoreceptor spectral sensitivities for both the VS and UVS avian visual systems, corrected for transmission of associated oil droplets from (Endler and Mielke 2005).

The model assumes that discriminability is limited by photoreceptor noise, represented by the noise-to-signal ratio (Weber fraction, ω_i). Under bright illumination conditions, the Weber fraction can be calculated by

$$\omega = \frac{v_i}{\sqrt{\eta_i}}. \tag{1}$$

where v_i is the noise-to-signal ratio of a single cone and η_i is the number of photoreceptors of type *i*. We assumed that $\omega_i = 0.1$ for the long-wavelength sensitive (LWS) cone (Vorobyev et al. 1998; Siddiqi et al. 2004) and derived values of ω_i for remaining photoreceptor classes from the equation above using a ratio of 1 UVS: 2 short-wavelength sensitive (SWS): 3.4 medium-wavelength sensitive (MWS): 3 LWS for the 4 avian photoreceptor classes of an UVS visual system and 1 VS: 1.4 SWS: 2 MWS: 2.6 LWS for the 4 avian photoreceptor classes of a VS visual system. These ratios are the mean ratios for birds of the 2 visual system types from Hart (2001). For achromatic or "brightness" contrast (f_D), we assumed that $\omega_i = 0.05$ for the double cone (Siddiqi et al. 2004).

To verify that the orange and white "flipped" lizards were more conspicuous than upright, cryptically colored lizards, we first derived an overall measure of conspicuousness for each lizard type by taking the average contrast of the color patches, weighted by the proportion of each color patch (Heinsohn et al. 2005). Proportions used were derived from analysis of digital photographs of 18 wild-caught females (Chan et al. 2009) and were 0.95 brown and 0.05 black for the cryptic lizards and 0.70 orange and 0.30 white for the flipped lizards.

Predation experiments

We conducted predation experiments at 6 sites on Lake Eyre, separated by a minimum of 2 kms (Supplementary Figure S1) and one site at Muloorina Station Borehole. Of the 200 models put out at each of the 7 sites, 100 were placed in normal upright posture (cryptic) and 100 were flipped over in rejection posture exposing their orange ventral surface (orange; Figure 1). Models were arranged in 4 transects of 50 models of alternating color types placed approximately 5 m apart. The transects were randomly placed in different orientations (Supplementary Figure S1). Models were anchored to the ground using a tent peg (completely submerged in the sand) and clear fishing wire. Models were only put out on days with suitable weather conditions for *C. maculosus* to be active (maximum temperatures >30 °C and not overly windy or overcast). All models were out by 9 AM and were taken in by 4:30 PM the following afternoon, corresponding to emergence and retreat times of *C. maculosus* (Mitchell 1973). In total, 100 models of each treatment (orange and cryptic) were put out at each of the 7 sites for 2 days amounting to a total of 1400 model days per treatment. There are no known nocturnal predators of *C. maculosus* (Mitchell 1973); however, we confirmed this by conducting an overnight pilot study at site 1 (Supplementary Figure S1), during which no predator attacks were detected.

Models were examined for attack marks (indentations in the plasticine) as they were collected. We photographed each attacked model and recorded model color (cryptic or orange) and location along the transect. We categorized attacks as definite bird, definite lizard (attacks from conspecifics), and definite predator (not necessarily a bird) or as ambiguous attacks. We repaired any damage caused by attacks and/or transport before the models were used again.

We included a site at the Muloorina Station borehole that, due to the constant presence of water, supports an unnaturally high density of birdlife including many raptor and corvid species (Supplementary Table S1). This enabled us to verify that low numbers of predator attacks at the lake sites were due to low predation pressure and not predator avoidance of models. At the borehole site, models were put out at 8:30 AM and checked for predator attacks on the same day at 5 PM due to the possibility that there were nocturnal predators. We checked and repaired the models again the following morning at 8:30 AM and collected at 5 PM that day, providing 2 days at the borehole site, as at lake sites.

We summed the number of each type of model attacked over the 2 days for each transect to derive attacks per model type (orange or cryptic) per transect (4 transects per site). We then tested whether there was a significant difference between the numbers of orange and cryptic models attacked using a 2-way analysis if variance (GLM, SYSTAT 12) with site, color, and their interaction as factors in the model.

RESULTS

Relative conspicuousness of lizards

The visual model confirmed that, to birds, *C. maculosus* females performing the flip-over rejection (referred to as orange throughout for simplicity) were consistently more conspicuous than unresisting females (referred to as cryptic throughout). Orange females had significantly higher overall chromatic (ΔS) and achromatic (f_D) contrasts against the dominant backgrounds at each site compared with cryptic females as perceived by birds with a VS visual system (Lake Eyre crust—chromatic: $F_{1,85} = 19.0$, $P < 0.001$, achromatic: $F_{1,85} = 46.4$, $P < 0.001$; Borehole sand—chromatic: $F_{1,85} = 15.3$, $P < 0.001$, achromatic: $F_{1,85} = 42.6$, $P < 0.001$; Figure 3) as well as birds with a UVS visual system (Lake Eyre crust—chromatic: $F_{1,85} = 26.2$, $P < 0.001$, achromatic: $F_{1,85} = 46.4$, $P < 0.001$; Borehole sand—chromatic: $F_{1,85} = 21.6$, $P < 0.001$, achromatic: $F_{1,85} = 42.9$, $P < 0.001$). The same was true for all other Lake Eyre and borehole backgrounds ($P < 0.01$ for all contrasts) with the exception of Lake Eyre sand where orange females did not differ significantly from cryptic females in their achromatic contrast (VS visual system: $F_{1,85} = 3.76$, $P = 0.056$; UVS visual system: $F_{1,85} = 3.76$, $P = 0.056$).

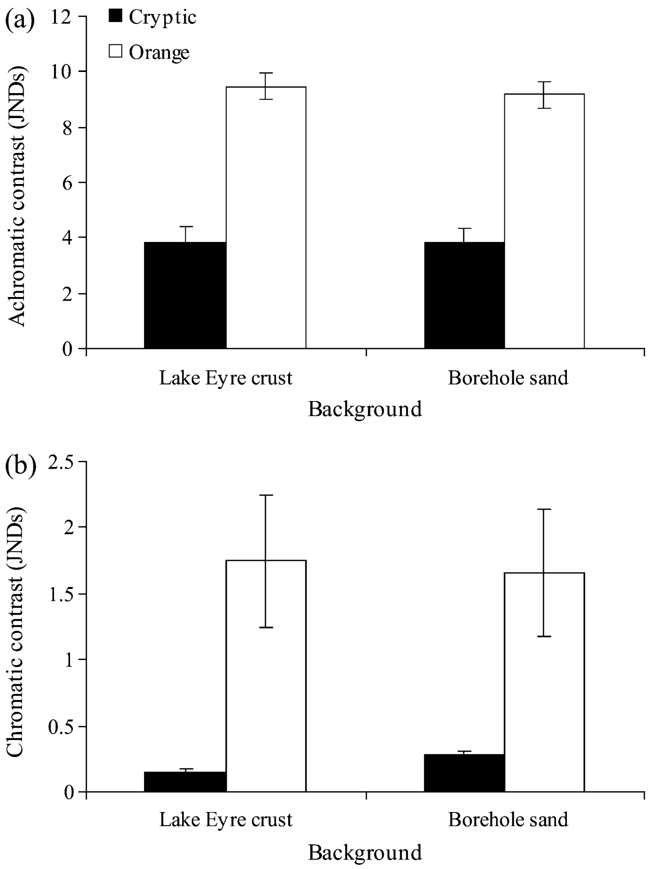

Figure 3
Mean (±SE) (a) chromatic and (b) achromatic overall contrasts of the ventral coloration of resisting *Ctenophorus maculosus* females (orange) and dorsal coloration of nonresisting *C. maculosus* females (cryptic) against Lake Eyre crust and borehole sand as perceived by an avian predator with a VS visual system. Contrasts are in units of just noticeable differences.

Comparison of models to lizards

The model materials closely resembled colors of real lizards to birds with both VS and UVS visual systems as viewed against the dominant background (Lake Eyre crust; Table 1). The same was true for the dominant background at the borehole site (Supplementary Table S2). There were no significant differences in either the chromatic or achromatic contrasts of real lizards against the background compared with that of model lizards against the same background. This was true for Lake Eyre crust, borehole sand, and all other Lake Eyre or borehole backgrounds with the exception of Lake Eyre sand where white model materials exhibited higher chromatic contrast than the white ventral coloration of the lizards ($F_{1,21} = 8.44$, $P = 0.008$).

Attacks on models

We were interested in attacks by visual predators, so only definite bird attacks were included in the analysis. We confirmed that attacks were from avian predators by examining marks left in the plasticine coating the models. Bird attacks left talon marks and clear V or U shaped beak marks (Brodie 1993;

Table 1

Comparison of model and lizard contrasts to the dominant Lake Eyre crust background for each color patch

Visual system	Contrast	Color patch	F_{df}	P
VS	Chromatic	Brown	$0.002_{1,39}$	0.969
		Black	$0.871_{1,16}$	0.365
		White	$0.006_{1,21}$	0.938
		Orange	$0.164_{1,8}$	0.696
	Achromatic	Brown	$0.004_{1,39}$	0.948
		Black	$0.982_{1,16}$	0.336
		White	$2.18_{1,21}$	0.155
		Orange	$1.56_{1,8}$	0.248
UVS	Chromatic	Brown	$0.069_{1,39}$	0.794
		Black	$0.776_{1,16}$	0.391
		White	$0.121_{1,21}$	0.731
		Orange	$0.178_{1,8}$	0.684
	Achromatic	Brown	$0.004_{1,39}$	0.948
		Black	$0.982_{1,16}$	0.336
		White	$2.18_{1,21}$	0.155
		Orange	$1.56_{1,8}$	0.248

df, degrees of freedom.

Castilla and Labra 1998), whereas attacks from conspecifics were characterized by regular indentations from teeth (Supplementary Figure S2). Overall predation at the lake sites was low with only 20 of 2400 models (200 models put out for 2 days at each of 6 Lake sites) attacked by birds (0.83%). In comparison, predation at the borehole was relatively high with 38 of 400 models (200 models put out for 2 days at one site) attacked by birds (9.5%). When including the borehole site in the analysis, cryptic models were attacked by birds significantly more often than orange models ($F_{1,42}$ = 5.19, P = 0.028; Figure 4a). There was also a significant difference between sites ($F_{6,42}$ = 5.76, P < 0.001) and no significant interaction between site and color ($F_{6,42}$ = 1.71, P = 0.142), indicating that cryptic models were consistently attacked more often across all sites. Results were qualitatively the same when the borehole site was excluded from the analysis (color: $F_{1,36}$ = 6.26, P = 0.017; site: $F_{5,36}$ = 2.66, P = 0.038; color × site: $F_{5,36}$ = 2.27, P = 0.068).

Conspecific lizards also attacked both orange and cryptic models at the lake sites. *C. maculosus* attack marks were generally located on the head and neck of the models and are easily distinguished from those of a potential lizard predator, *V. gouldii*, by the head shape, size, and dentition. *C. maculosus* males are highly territorial and engage in physical contests involving biting (Olsson 1995b); therefore, lizard attacks may be territorial or, due to the location of attack marks, may be attempted mating grasps. Overall, 66 of 2400 models were attacked by lizards (2.75%). For lizard attacks, there was a significant interaction between color and site ($F_{5,36}$ = 3.88, P = 0.006). Cryptic models were attacked by lizards significantly more than orange models at sites 1 ($F_{1,6}$ = 6.40, P = 0.045), 2 ($F_{1,6}$ = 11.3, P = 0.015), 3 ($F_{1,6}$ = 22.0, P = 0.003), and 5 ($F_{1,6}$ = 6.82, P = 0.040) but not sites 4 ($F_{1,6}$ = 0.000, P = 1.000) and 7 ($F_{1,6}$ = 0.429, P = 0.537; Figure 4b).

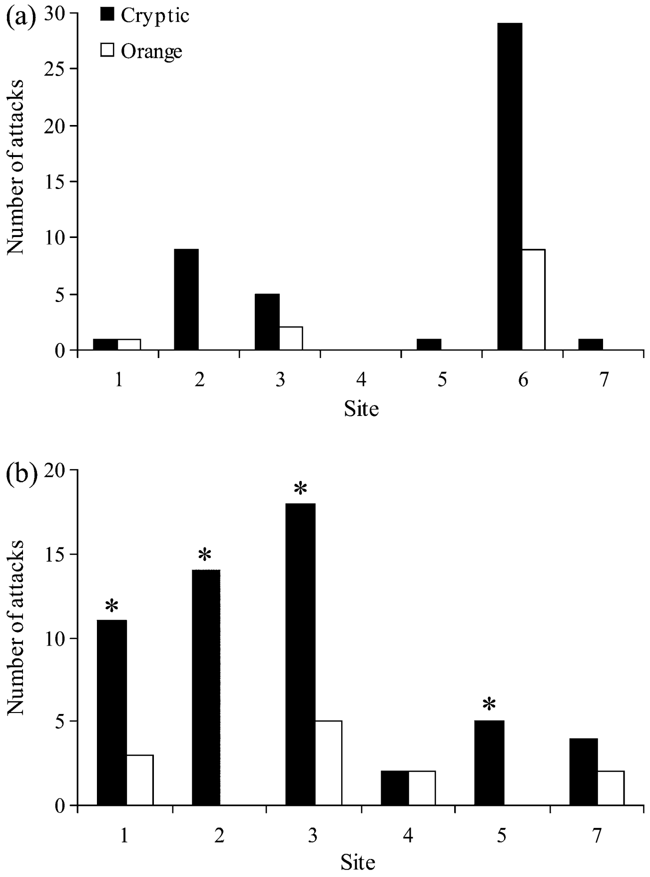

Figure 4

(a) The number of cryptic and orange models attacked by avian predators at each of the 7 field sites. Sites 1, 2, 3, 4, 5, and 7 are lake sites, whereas site 6 is at the Muloorina Station borehole. (b) The number of cryptic and orange models attacked by *Ctenophorus maculosus* at the 6 lake sites excluding the borehole site, where *C. maculosus* are not found. Only unambiguous attacks are included. Asterisks denote a significant difference in the number of attacks on model types (P < 0.05).

DISCUSSION

We tested the hypothesis that flipped over, resisting *C. maculosus* females are more conspicuous to visual predators and therefore more likely to be attacked. We first tested whether resisting (orange) and nonresisting (cryptic) females were differentially conspicuous to potential avian predators using a model of bird vision (Vorobyev and Osorio 1998). Based on this model, orange females were much more conspicuous to avian predators, contrasting more against their background, both chromatically and achromatically, than cryptic females. To investigate the second part of our hypothesis, that orange females are more likely to be attacked, we compared the frequency of attacks on orange and cryptic models. Overall predation at the lake sites was low. However, at the borehole, where predator density was high, attack frequency was also high, suggesting that the low number of attacks at the lake sites was most likely due to low predator density and not predator avoidance of models. We found that compared with cryptic models, orange models were less likely to be attacked at both the lake and borehole sites, despite being more conspicuous. Both birds and conspecific lizards attacked both cryptic and orange models and *C. maculosus* males displayed toward both model types. Furthermore, spectral analysis showed no significant difference between orange or cryptic coloration of model and real lizards as perceived by birds. For these reasons, it is reasonable to assume that both cryptic and orange model types were effective representations of *C. maculosus* and differences in predation were due to predator preference and not inferior quality of orange models.

A possible explanation for lower predation risk for orange females is that unpalatable prey sometimes signal their unprofitability to predators through the use of bright warning coloration or aposematism (Mappes et al. 2005). Although

C. maculosus is not unpalatable, it could exhibit Batesian mimicry, where a palatable species mimics an unpalatable species with which predators are familiar (Mappes and Alatalo 1997). However, this seems highly unlikely as a mimic must closely resemble the aposematic species in order to be an effective defense (Mappes and Alatalo 1997) and there does not appear to be any aposematic species similar to *C. maculosus* within its distribution. A more plausible explanation for the higher attack rate on cryptic models may be dietary conservatism (e.g., Thomas et al. 2003) or frequency-dependant predation, where predators consume disproportionately more of a prey type when it is common (Punzalan et al. 2005). Relative to orange *C. maculosus* females, cryptic females are much more common, both spatially and temporally. This is because females only exhibit orange color patches when flipped over and the flip-over rejection is only performed during the breeding season by unreceptive females when rejecting courting males (Olsson 1995a). Furthermore, females only flip over for short periods of time. The average flip-over duration of females during behavioral experiments is approximately 12 s (McLean CA, unpublished data). Consequently, predators are rarely (if ever) exposed to orange females. Predators may also not recognize flipped-over females as prey due to their unusual posture. Furthermore, the unfamiliar shape of the orange and white color patterns could also affect predator perception of prey. The orange color patches may break up the outline of the lizard, making it harder for predators to recognize it as prey. Breaking up the body's outline is a key feature of disruptive camouflage (Stevens and Merilaita 2009). Further study would be needed to tease apart the effects of color, posture, and pattern on predation risk.

Frequency-dependant predation where predators avoid rare prey is a well-documented phenomenon commonly referred to as apostatic selection (Clarke 1962; Bond and Kamil 1998). Predators may consistently choose the most common prey and avoid rare prey, even if they are much more conspicuous. This has been confirmed by several studies presenting wild bird predators with artificial prey (Thomas et al. 2003, 2004). One mechanism explaining apostatic selection is "search image formation," first proposed by Tinbergen (1960) as an explanation for disproportionately higher predation of common prey than rare prey by great tits (*Parus major*) and subsequently confirmed by numerous studies (e.g., Pietrewicz and Kamil 1979; Gendron 1986; Blough 1991). Search image can be defined as a selective search for a particular prey type, which increases the probability of detecting that prey type while decreasing the probability of detecting any other prey types (Dukas 2004). When prey is cryptic, dividing attention among multiple prey types reduces foraging efficiency (Dukas 2004). By focusing on a single cryptic prey type, predators bypass other prey types but increase their overall foraging efficiency (Dukas 2004). Theoretically, a predator would benefit by forming a search image of *C. maculosus* as the species is highly cryptic and difficult to detect. Significantly lower attacks on orange models could then be explained by the predator overlooking prey types other than that for which it has formed a search image (i.e., the cryptic form).

Testing predation risk using static models has some limitations. If predators rely on movement to detect prey, they may not attack a motionless model. Thus, absolute predation rates for models may not be representative of those for live lizards. Instead, experiments using models provide estimates of relative, rather than absolute, predation risk for different prey types. Although our results clearly show that the conspicuous orange color pattern of rejecting females does not increase the likelihood of predation relative to the cryptic coloration of upright females, if rejecting female lizards move substantially more than nonrejecting females, our experiments may underestimate the relative cost of rejection. However, females remain motionless for up to a minute while flipped over, whereas flipping itself takes less than a second suggesting that the predation cost of the flip-over behavior is likely to be incurred primarily through increased conspicuousness rather than movement. The use of models also cannot account for antipredator behavior such as fleeing, seeking shelter, or defensive behaviors. However, as the most common antipredator behavior employed by *C. maculosus* is to crouch down and remain motionless (Mitchell 1973), the 2 prey types (orange and cryptic) are unlikely to differ in antipredator behavior. Furthermore, an experimental study of predation on one lizard species found that predation risk is determined by the predator's probability of detecting a potential prey item not its probability of capturing the prey item after detection (Schwarzkopf and Shine 1992). For these reasons, it was appropriate to use static models for this study.

The flip-over rejection of *C. maculosus* has been widely cited as a costly resistance strategy as it increases the female's conspicuousness to predators and is therefore thought to increase predation risk. Indeed, female resistance in many species could influence predation risk (Arnqvist and Rowe 2005). However, results of this study provide a cautionary lesson when inferring predation costs of resistance. In *C. maculosus*, these costs are likely to be lower than previously assumed and resistance may even reduce predation risk. Flipping over, however, is very unlikely to be used as an antipredator tactic as it appears to be the rarity of the behavior, rather than the behavior per se, that confers the initial selective advantage. Flipping over is also unlikely to carry energetic costs as females should expend less energy rolling over than they would running away from or even threatening a courting male. By contrast, the costs of mating to females of this species are likely to be relatively high (Olsson 1995a). Consequently, it appears that female resistance has evolved because the fitness benefits gained from preventing superfluous copulations outweigh the costs associated with resistance, as predicted under sexual conflict.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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