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CUIDADO MATERNAL E CRIPTICIDADE EM *ULOBORUS* SP. (ARANEAE, ULOBORIDAE)

Aline Leles Nascimento

2015

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Dissertação apresentada à Universidade Federal de Uberlândia, como parte das exigências para obtenção do título de Mestre em Ecologia e Conservação de Recursos Naturais.

Orientador:
Marcelo de Oliveira Gonzaga

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Muito obrigada.

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RESUMO: A interação predador-presa desempenha um papel fundamental na evolução de mecanismos adaptativos e posturas agressivas em diferentes grupos animais. A partir disso, organismos com colorações e comportamentos que reduzem o risco de detecção por inimigos naturais possuem uma enorme vantagem seletiva em relação aos que não possuem essa característica. Espécies com cuidado maternal podem maximizar o esforço reprodutivo carregando e cuidando de ovos e filhotes. Além disso, comportamentos agressivos contra predadores e outros inimigos naturais parecem ser essenciais para evitar o ataque de inimigos e aumentar a sobrevivência dos filhotes. A partir disso, o objetivo deste trabalho foi descrever os padrões na construção de teias durante o comportamento maternal, além de analisar a influência do investimento prévio na ninhada e tamanho das fêmeas nas reações agressivas contra estímulos artificiais simulando eventos de predação dos ovos. Foi analisado também, a partir da perspectiva de visão de inimigos naturais, se a coloração de aranhas e ootecas são semelhantes entre si e em relação aos galhos onde a teia é fixada. Foi observado que as aranhas constroem teias modificadas durante o período de cuidado, nas quais não são capazes de capturar presas e permanecem em uma postura críptica alinhada com a ooteca tubular. Aranhas com ootecas responderam agressivamente aos estímulos e aranhas sem ootecas fugiram ou evitaram a fonte de distúrbios. As respostas agressivas, no entanto, foram independentes do tamanho da ninhada e do tamanho corporal das fêmeas. As análises de coloração demonstraram que himenópteros e aves não conseguem diferenciar as cores de aranhas e ootecas e de aranhas e galhos, denotando a importância da coloração na detecção de *Uloborus* sp.

Palavras-chave: investimento parental, camuflagem, modelos visuais.

ABSTRACT

Predator-prey interactions play a key role in the evolution of adaptive mechanisms and aggressive postures in different animal groups. From this, organisms with colors and behaviors that reduce the risk of detection by natural enemies have a huge selective advantage over those who do not have this attribute. Species with maternal care can maximize their reproductive effort protecting eggs and offspring. In addition, aggressive behaviors against predators and other natural enemies appear to be essential to avoid the enemies' attacks and increase offspring survivorship . Thus, in this study we aim to describe web building patterns during maternal behavior, and the influence of previous investment in reproduction and spider size on aggressive behavioral responses against artificial stimuli simulating attacks of predators. We also examined, from the perspective of view of natural enemies, if the colors of spiders and egg sacs are similar to each other and to the branches in which the webs are attached . We observed that females build modified webs during the period of egg sac protection, in which they are unable to capture prey and remain in a cryptic posture, aligned with their tubular egg sacs. Spiders carrying egg sacs showed aggressive responses to artificial stimuli and spiders without egg sacs always ran away or avoided the source of disturbance. Aggressive responses, however, were independent of clutch size and female body size. . Color analyzes showed that Hymenoptera and birds can not differentiate the colors of spiders and egg sacs, and of spiders and branches as well, showing the importance of color in decreasing detection from this specie.

Keywords: parental investiment, camouflage, visual models.

INTRODUÇÃO GERAL

A interação predador-presa desempenha um importante papel na evolução de mecanismos adaptativos, tais como cripticidade, aposematismo, posturas corporais protetivas, defesas químicas, dentre outros (SIH, 1987; LIMA; DILL, 1990). De maneira geral, um organismo pode ser considerado críptico quando o seu padrão de coloração é semelhante a uma amostra aleatória do padrão de fundo percebido pelo predador em determinadas condições fisiológicas, visuais e ambientais (ENDLER, 1978) e esta estratégia pode elevar consideravelmente o fitness do indivíduo. Vignieri et al. (2010), por exemplo, demonstraram que a correspondência na coloração dos roedores pertencentes ao gênero *Peromyscus* em relação ao fundo onde estão inseridos é dirigida por predadores visualmente orientados e que isso confere uma enorme vantagem seletiva a esses organismos em ambientes naturais.

Espécies com colorações crípticas ou menos conspícuas são frequentemente associadas a posturas que facilitam a semelhança com elementos da vegetação de fundo onde estão inseridos. Em aranhas, *Arachnura scorpionides* possui o formato do corpo e coloração bastante semelhante a galhos e folhas secas enquanto *Hyptiotes paradoxus* possui uma aparência que se assemelha a ramos secos de abeto (STERN; KULLMANN 1975). A coloração e postura apresentadas por esses indivíduos parecem ser essenciais na proteção contra predadores visualmente orientados e ter um papel essencial na história de vida desses organismos.

Alguns membros da família Uloboridae, especialmente pertencentes aos gêneros *Miagrammopes* e *Uloborus*, apresentam o padrão críptico de coloração corporal bastante semelhante ao de suas ootecas, que são longas e tubulares (LUBIN et al., 1978, CUSHING, 1989), e a posição de alinhamento apresentada por eles parece fornecer uma importante vantagem na proteção dos ovos contra predação (CUSHING, 1988). Além de aspectos envolvendo a coloração, o cuidado maternal em aranhas pode abranger desde o envolvimento dos ovos em camadas de seda até a proteção e alimentação da ninhada nos primeiros estágios de desenvolvimento (GONZAGA, 2007). Inúmeros benefícios podem ser obtidos por filhotes que estão sob cuidado da mãe, tais como a regulação de fatores abióticos (NORGAARD, 1956; HUMPHREYS, 1974), o fornecimento alimento aos filhotes (KULLMANN, 1972; BURSKRIK, 1981), o aprovisionamento de nutrientes em ovos tróficos (GONZAGA, 2007), a matrifagia (BRISTOWE, 1958; KIM et al., 2000), além da proteção ativa contra inimigos naturais (LUBIN, 1974; FINK, 1986; GONZAGA, 2007).

A partir disso, a presente dissertação tem por objetivo elucidar questões referentes ao cuidado maternal e a coloração críptica apresentada por *Uloborus* sp. em posse de sua ooteca. O primeiro capítulo descreve mudanças na construção da teia durante o período de cuidado com os filhotes, com importantes consequências na sobrevivência das mães, além de comportamentos defensivos da espécie em período de cuidado maternal ou não, e por fim, relaciona esses comportamentos com o tamanho da ninhada e o tamanho da fêmea. O capítulo 2 descreve, por meio de modelos visuais de predadores, como a aranha e sua ooteca são visualizadas por himenópteros e aves e se existe diferença também, sob a perspectiva de visão de predadores, na coloração de ambos em relação ao padrão de coloração dos galhos onde a teia é fixada.

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Capítulo 1

Maternal defensive behaviors of *Uloborus* sp. (Araneae, Uloboridae): an analysis of the influence of clutch size and female size on aggressiveness and behavioral repertory

Maternal defensive behaviors of *Uloborus* sp. (Araneae, Uloboridae): influence of clutch size and female size on female aggressiveness and behavioral repertoire

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Abstract. Maternal care in spiders often involves behaviors associated with the protection of eggs and spiderlings against parasitoids and predators (including conspecifics). The females of several species have been documented to move their egg sacs away from natural enemies or to invest in active defense behavior against web invaders, such as parasitoid wasps or araneophagic spider species, to protect their brood. In this study, we present behavioral observations of protective behavior by *Uloborus* sp. females carrying eggs sacs. We also investigated whether brood size (past reproductive investment) and female size influence the degree of female aggressive behavior against an artificial source of disturbance. Females carrying egg sacs almost immediately perceived and reacted aggressively against the artificial stimulus, whereas females without egg sacs moved away or ran to the web margins, avoiding the source of disturbance. The aggressive response was independent of clutch size and female body size, indicating that all females will risk interacting with potential agents of egg mortality, even after producing their first eggs. This consistent response by all females with egg sacs may be important for reducing the incidence of attack by the egg predator *Bathyzonus* sp. (Ichneumonidae).

Keywords: Maternal care, aggressive behavior, reproductive investment

Introduction

According to Trivers (1972), parents should adjust current care in relation to past investment to minimize the loss of reproductive effort. Thus, in situations where mothers could efficiently prevent egg loss due to agonistic interactions with predators and parasitoids, intensive care is expected, especially after large investment in egg production. However, maternal care is costly, because females (1) usually reduce foraging activity, limiting the amount of resources available for future reproduction events, and (2) often risk the possibility of producing a new brood to protect the existing brood in dangerous situations (Clutton-Brock 1991, Buzatto *et al*. 2007). Therefore, decisions about parental investment must reflect a balance between costs (e.g., energy loss, risk of injuries) and benefits (e.g., probability of brood survivorship) of each behavior and also past investment in reproductive events (e.g., the value of the protected brood).

Maternal care in spiders always involves the construction of a protective silk structure for the eggs, which is placed in suitable sites for optimal development (Austin 1985, Hieber 1992, DeVito & Formanowicz 2003, Pike *et al.* 2012, Yip & Rayor 2014). The egg sac often operates as a very complex barrier, and is sometimes composed of several layered sheets containing fibers from different silk glands (Lepore *et al.* 2012, Gheysens *et al.* 2005). The egg sac may also contain additional defensive systems (e.g., the incorporation of urticating hairs into the silk, see Marshall & Uetz 1990) or may remain concealed within the detritus columns of stabilimenta (Gonzaga & Vasconcellos-Neto 2012), curled dead leaves (Moya 2010), folded green leaves (Zanatta 2013), under rocks (Pike *et al.* 2012), or within other types of shelters (see Manicom *et al.* 2008). The efficiency of the egg sac silk layers at maintaining appropriate temperature and humidity conditions (Opell 1984) and reducing the exposure of eggs to predators and parasitoids (Hieber 1984, Austin 1985, Hieber 1992) are fundamental for female spider reproductive success.

Covering the eggs in silk and placing the egg sac in a suitable site is certainly important; however, many species provide additional protection against predators and parasitoids during egg development (Fink 1987, Whitehouse & Jackson 1998, Gonzaga & Leiner 2013). For example, Gonzaga & Leneir (2013) showed that the survivorship of *Helvibis longicauda* (Theridiidae) eggs and spiderlings depends on active protection by their mothers against conspecific web invaders. *Delena cancerides* (Sparassidae) mothers also are effective at chasing and killing potential predators introduced experimentally in their nests (Yip & Rayor 2011).

Within the orb-weaver family Uloboridae, the described protective behaviors of mothers during the egg sac guarding period include (1) the removal of egg sacs to the edge of webs when under threat *Philoponella republicana* (Hoffmaster 1982), (2) the placement of the egg sac in a protected area near the orb (usually under a rock or log) by *P. oweni* (Smith 1997), and (3) the direct attack of parasitoid wasps by *Uloborus glomosus* (Cushing 1989). During these attacks, *U. glomosus* females have been observed to jerk the webs and making sweeping motions in response to the parasitoid wasp *Arachnopteromalus dasys* (Pteromalidae) crawling on the egg sacs (Cushing 1989, Cushing & Opell 1990). Yet, Smith (1997) observed the same parasitoid species attacking the egg sacs of *Philoponella arizonica* and *P. owenii*, but these two spider species did not respond aggressively to protect their eggs. The absence of defensive reactions against *A. dasys* was also observed by Santos & Gonzaga (in prep.) for a new genus of Uloboridae from southeastern Brazil.

In this study, we evaluated maternal care decisions in a species of the family Uloboridae, taking previous investment in reproduction (number of eggs in the egg sac) and mother body size into account. Mother body size may be correlated to (1) the risk of injury and/or death during agonist interactions with potential predators and parasitoids, (2) the probability of success during a confrontation, (3) the energetic cost of egg protection, and (4) the amount of energetic resources available for further egg production. We also described the behavioral repertoire of females during egg sac protection and the frequency of predator wasps attacking the egg sacs.

Material and methods

Study site

Spiders were collected in November 2014 in a *Eucalyptus* plantation in Fazenda Nova Monte Carmelo, property of Duratex S.A. (18° 45' 11" S, 47° 51' 28" W), Estrela do Sul, Minas Gerais, Brazil. Areas covered by introduced *Eucalyptus* are interspersed with fragments of native savanna (Cerrado) in Fazenda Nova Monte Carmelo. *Uloborus* sp. primarily construct their webs on the lower branches of *Eucalyptus,* close to the litter layer (0–50cm).

Study species

The genus *Uloborus* is currently composed of 80 species, 16 of which occur in South America, with only four of these species occurring in Brazil; specifically, *U. ater* Mello-Leitão 1917, *U. minutus* Mello-Leitão 1915, *U. niger* Mello-Leitão 1917, and *U.*

tetramaculatus Mello-Leitão 1940. All of the Brazilian *Uloborus* species have been described by Mello-Leitão based on female specimens alone, with three of these species being collected from southeastern Brazil. The descriptions of these species are restricted to color patterns (Mello-Leitão 1915, 1917); thus, it remains unclear as to whether the species studied in Fazenda Nova Monte Carmelo is actually one of these four species. A taxonomic revision of South American uloborids is required to resolve these problems, and allow progress on ecological studies on this group.

Procedures

All spiders and egg sacs were collected in the field and on the same day in November 2014. We compared the web construction patterns of females with and without egg sacs by analyzing photographs of webs taken before sampling.

We collected 28 females with egg sacs. Each female was maintained in a plastic container (2500 ml) with *Eucalyptus* sticks to allow web construction. After web construction (48 h after introduction to containers), we performed artificial simulations of wasp attacks by touching the egg sacs gently with a brush. Artificial stimuli are often used to simulate prey items, potential predators or parasitoids in experiments with spiders (e.g., Tolbert 1975, Coyle 1986, Cushing & Opell, 1990, Mooney & Haloin 2006). However, while this method is inefficient at producing vibrational stimuli similar to those produced by wasps, we assumed that spiders would attack any source of potential risk to their eggs.

We filmed the reactions of all spiders to the stimulus for up to 5 minutes. When there was no response, we continued recording for at least 10 minutes. After this procedure, we kept the egg sacs in the containers until the spiderlings emerged. The video recordings were used to document (1) the time at which females first reacted, (2) the time at which females attacked the source of disturbance, and (3) the behavioral repertoire of females throughout the experiment. We also documented the presence or absence of parasitoid and predator larvae already inside eggs after the completion of the behavior response tests, and the number of spiderlings that emerged from each egg sac. The number of eggs and the total body length of spiders were determined using a stereomicroscope (Leica 250C, Wetzlar, Germany) equipped with a SmartTouch controller, a Leica DFC 290 camera, and an LAS Application Suite assembling Interactive Measurement Module (Leica). We assembled an ethogram depicting the behavioral sequences, and recorded the number of spiders performing each behavior.

We performed a linear regression between the variables to analyze how aggressiveness, expressed by the time elapsed from the introduction of the stimuli to the first spider reaction (reaction time) and by the time elapsed until the attack against the source of disturbance (attacking time), was related to clutch size and spider size. Data normality was verified by the Shapiro-Wilk test (Razali & Wah 2011). As the maximum reaction time was 32 seconds and each video lasted 100 seconds, we used the value of 100 seconds to represent females that did not respond to stimulation. The same value was used to represent females that did not attack. The response of females with and without egg sacs was compared by a t-test, based on the reaction time after the stimulus.

Results

Before egg-laying, *Uloborus* sp. females remain at the hub of their horizontal orb webs in a typical resting position, extending the first and second pair of long and slender legs to the front of the bodies (Fig. 1A–C). Spiders only abandon this position when capturing prey or copulating. However, the webs of adult females carrying egg sacs differ to those of females without egg sacs. When carrying an egg sac, females build webs with widely spaced threads, lacking spirals and regular radii distribution (Fig. 1D–E). This modified web design is not suitable for intercepting and retaining insects, but allows the egg sac to be aligned with the mother, and suspended away from potential predators, such as ants (Fig. 2). When resting on these webs, females are positioned with the first two pairs of legs stretched forward and the egg sacs aligned with the abdomen. The overall appearance resembles a suspended twig, especially at a certain distance (Fig. 2A). The *Uloborus* sp. egg sac is tubular and elongated, containing an average of 136 eggs (N = 20). After leaving the egg sac, spiderlings remain aggregated around the mother for about two days, after which they build their own webs that are initially attached to the web of their mother (Fig. 2B).

The female behavioral repertoire after the initial stimulus included: (1) placing tension on the web threads (the spider used the first and second pairs of legs to extend the web thread connected to the egg sac); (2) vibrating the web (the spider remained in its original position, but shook the web vigorously); (3) attacking the source of disturbance (the spider turned in the direction of the brush and ran towards it); (4) inspecting the egg sac (the spider walked along all of the egg sac extensions several times, touching the sack surface with its legs and chelicerae). Placing tension on the web threads and vibrating the web were most commonly documented behaviors, followed by direct attack toward the source of disturbance and inspection of egg sacs (Fig. 3). From the 28 females analyzed, only one did not respond to stimulation, remaining in the resting position throughout the assay. In the assays of spiders without egg sacs, the females performed the escape behaviors from potential enemies, including moving a few centimeters away or running to the web margins. Again, only one spider showed no reaction to the stimulus.

After the experiments we opened all of the egg sacs and found that the sac belonging to the female that failed to react was occupied by the larva of an egg predator wasp. This larva belonged to a new undescribed species of *Bathyzonus* (Ichneumonidae) (Fig. 4). After examining 60 egg sacs to evaluate the frequency of parasitism or predation, we found only one other specimen of *Bathyzonus* sp. The incidence of egg sacs being subject to predation was just 1.67%.

The body length of female spiders was not related to reaction time ($R^2 = 0.05$; $p = 0.27$) or with the time until females initiated attack ($R^2 = 0.0009$; $p = 0.87$). In addition, spiders with larger clutches did not react faster to the stimulus compared to those with smaller clutches ($R^2 = 0.06$; $p = 0.178$). The time until females initiated attack was also independent of clutch size ($R^2 = 0.053$; $p = 0.234$). In addition, there were no significant differences between the reaction time of spiders with and without egg sacs ($t = -0.656$; df = 40; $p = 0.5$).

Discussion

Webs constructed by females during the period of maternal care appear to be completely ineffective at trapping and retaining insects.. These webs resemble simple “skeleton” webs constructed by other orb-weaver species during molting (Robinson & Robinson 1973, Gonzaga *et al.* 2010) and some modified cocoon webs spun by spiders attacked by ichneumonid parasitoids (Gonzaga et al. 2015). The absence of cribellate spirals and the presence of fewer radii may enhance web stability and tenacity, reducing damage that occurs when insects become trapped. These webs are also apparently less conspicuous to visually oriented predators. Moreover, less silk is used to build these modified webs compared to that used in normal orb-web construction, which may be crucial for preserving the energy reserves of females when guarding egg sacs. Females, however, are unable to capture prey while carrying egg sacs, allocating all their energy reserves to guarding the eggs. These costs may compromise future reproductive events and, perhaps, female survivorship.

Changes to web design during the reproductive period are relatively rare in spiders, with only a few cases being reported for orb-weavers (Higgins 1990, Sherman 1994). Cases where m aternal care is associated with a long period of food abstinence are also uncommon in orb web spiders, but have been extensively studied in wolf spiders (e.g., Nyffeler 2000). By analyzing the web construction of many spider species in the genus *Miagrammpes*, Lubin et al. (1978), reported that during the egg carrying period, *Miagrammopes simus* (Uloboridae) females do not build webs to capture insects. However, the authors recorded that another species of *Miagrammopes* maintains a cryptic posture and does not capture prey during the day, but then abandons the cryptic posture and spins a cribellate thread at night to forage.

In the current study, *Uloborus* sp. females carrying egg sacs reacted aggressively towards the source of disturbance, performing a sequence of behaviors very similar to those observed in *U. glomosus* (Cushing 1989, Cushing & Opell 1990). Cushing & Opell (1990) showed that, when disturbed by the wasp *A. dasys* (Pteromalidae), *U. glomosus* responded by jerking their webs and, sometimes, turning around and walking along the egg sacs, sweeping the surface with their front legs. However, the authors also observed that the spiders jerk the webs when spiderlings cause vibrations, suggesting that *U. glomosus* has a similar response to all stimuli perceived on the egg sac surface.

Besides jerking behavior, the responses of *Uloborus* sp. females also included aggressive attacks against the source of disturbance.

Uloborus sp. females responded to the artificial stimulus in four different ways; specifically, females tried to vibrate or place tension on the web threads to drive away the predator/parasitoid, after which they attacked the source of disturbance and inspected the egg sacs after the disturbance had stopped. Despite all of these behaviors, enemies may still gain access the egg sacs and prey on the eggs. In our study, one female showed no response (any reaction or attack) toward the source of disturbance. Offspring desertion is expected, and may represents an adaptive reproductive strategy, in which when parents forgo the costly and/or risky care of an unprofitable current brood to save resources or to increase their own survivorship probability for investing in a future reproductive event (Ward et al. 2009). Unlike spiders protecting their broods, females without egg sacs responded to the stimulus by moving away or running to the edge of the web. Thus, the jerking of threads by mothers and attacking the source of disturbance represent actions to protect eggs against predators or parasitoids.

Several studies on other taxonomic groups with extended maternal care have demonstrated a relationship between the intensity and duration of protective behaviors with the body size/condition of a mother, the value of the protected brood (number of individuals, proportion of mother's total reproductive capacity), and ability of a mother to produce effective protective actions (Montgomerie & Weatherhead 1988, Buzatto et al. 2007, Ward et al. 2009, Kazama et al. 2010). Our experiment showed that the protective behavior of *Uloborus* sp. is independent of the body size of a mother and number of eggs in the egg sac. It would be useful to determine whether these spiders are able to produce a new egg sac after the first reproductive event. The large costs and risks of protecting the first egg sac produced indicate that (1) maternal behavior is may be important for brood survivorship during egg phase, (2) females are restricted to one reproductive event, and (3) attacking to prevent egg mortality may enhance female fitness, because this behavior is independent of female body size.

Few studies have described the natural enemies of Uloborids in the published literature. Most studies provide information about attacks by the egg predator *A. dasys* on the egg sacs of several species. This predator has been documented to consume the eggs of *Octonoba sinensis* (Gordh 1976), *P. arizonica* (Smith 1997), *P. oweni* (Smith 1982, 1997), *U. glomosus* (Cushing 1989), an unidentified species of Uloboridae (Gordh 1983), a species from a new genus in southeastern Brazil (Santos & Gonzaga, in prep), and *O. sinensis* (Peaslee & Peck 1983). In the populations of some of these species, the incidence of *A. dasys* predation is extremely high, reaching 58% of all collected egg sacs (see Peaslee & Peck 1983). Among egg parasitoids, there is only one record of *Idris* sp. (Platigastridae) attacking the eggs of a *Uloborus* species that lives as a commensal in colonies of *Stegodyphus sarasinorum* (Eresidae) (Bradoo 1972). Here, we presented the first register of predation of an uloborid by a species of *Bathyzonus*, a genus with an unknown natural history.

In the current study, the proportion of *Uloborus* sp. egg sacs that had been attacked by the hymenopteran egg predator was very low when compared to the incidence of *A. dasys* predation observed in other species. The aggressiveness of *Uloborus* sp. against possible sources of egg mortality may contribute to this low incidence of attack. Alternatively, it may also be explained by a possible low density *Bathyzonus* sp. at the study site. Finally, this species may attack other uloborids (or even other groups of spiders) and may not be so efficient at locating the cryptic egg sacs of *Uloborus* sp.

Cushing & Opell (1990) suggested that the egg sac chains of *U. glomosus* function as cryptic devices making the spiders aligned with them less conspicuous to visual oriented predators and, consequently, less likely to show active avoidance behaviors when disturbed. The behavior of remaining aligned with the egg sac in a position that may difficult to a predator to identify the contour of the spider body has also been observed in the araneids *Cyclosa* (Gonzaga & Vasconcellos-Neto 2005) and *Allocyclosa* (Eberhard 2003), as well as in other uloborids (e.g., Opell 1988). This behavior may be a component of maternal care, as it reduces the probability of egg sacs being identified by predators, in addition to being an adaptation of mothers to reduce their own risk of predation during a period of immobility (and energy conservation) in their modified webs.

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Figure captions

Fig. 1 A: Female in a typical resting position; B–C:.Normal web; D–E: Web constructed during the period of maternal care

Fig. 2 A: Female positioning when protecting its egg sac; B: Spiderlings just after leaving the egg sac.

Fig. 3 A, C: Behavioral repertoire during egg sac protection by *Uloborus* sp. females, where 1 represents the resting position; 2 represents the position in which females place tension on the web and vibrate the web; 3–5 represent the attack time, 6–9 represent the inspection of egg sacs after the attack has ended.
B Behavioral repertoire in assays of adult females without eggs sacs.

Fig. 4 *Bathyzonus* sp. Egg predator found in the egg sacs of *Uloburus* sp.

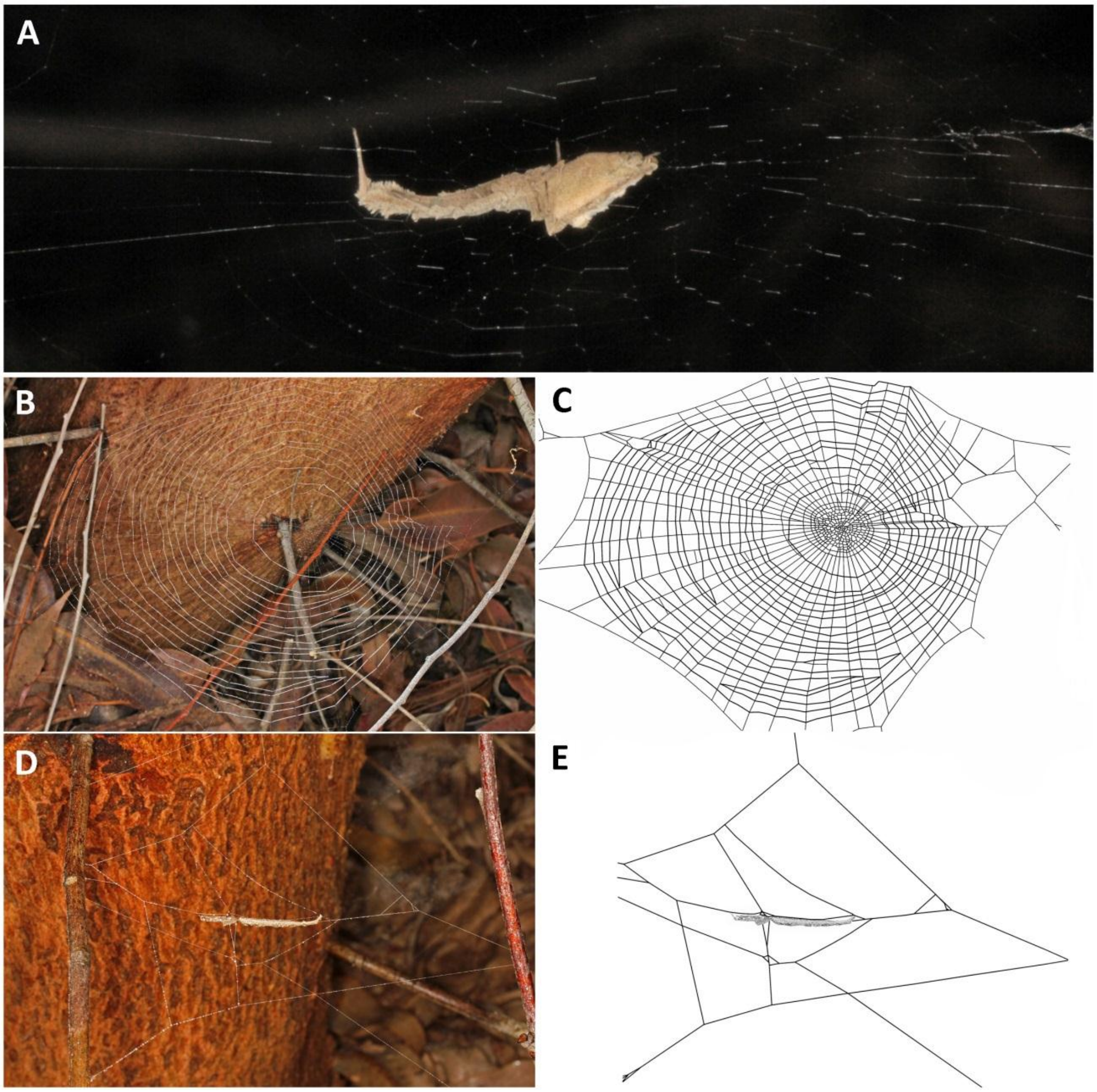

Fig 1

Fig 2

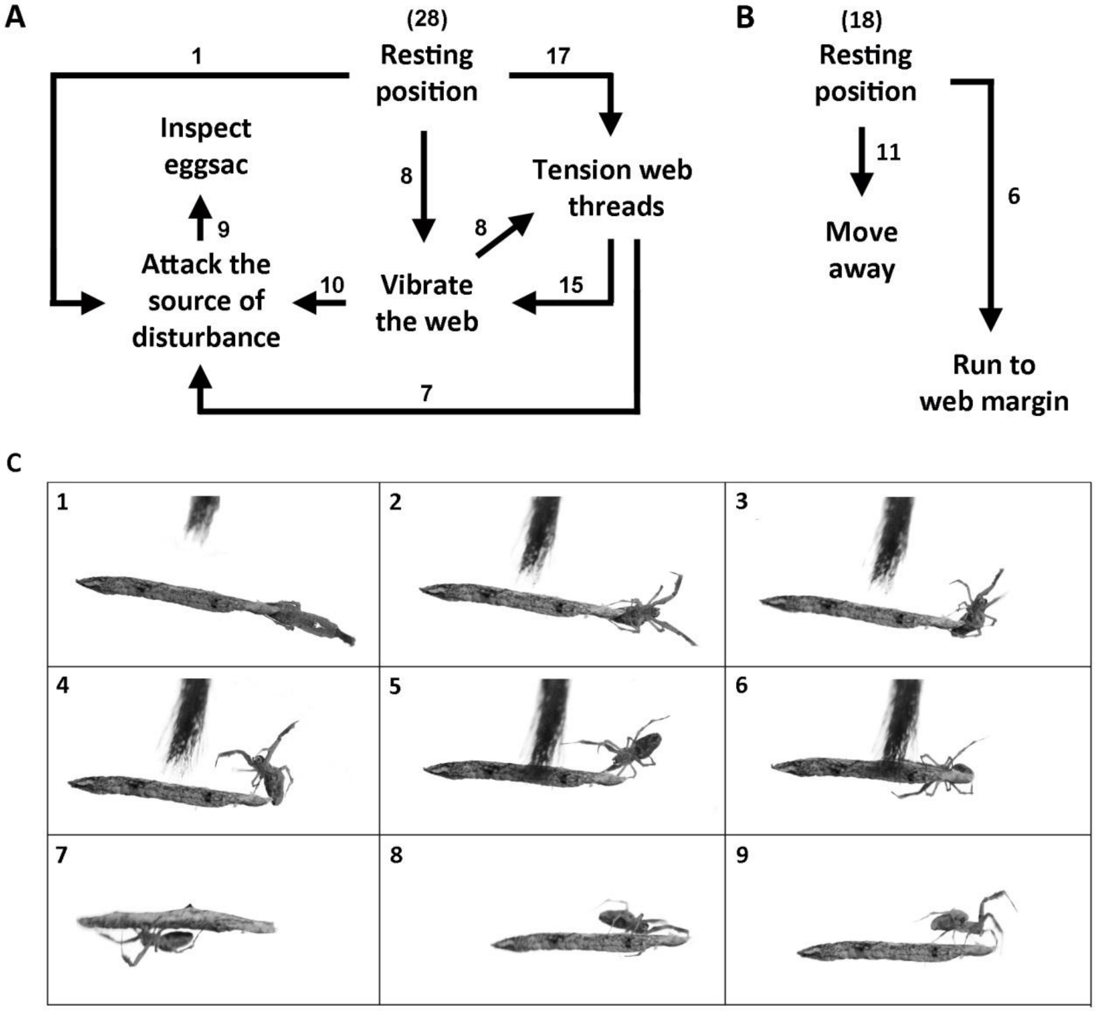
A
(28)
Resting position
1
17
Inspect eggsac
8
Tension web threads
9
8
Attack the source of disturbance
10
Vibrate the web
15
7
B
(18)
Resting position
11
6
Move away
Run to web margin
C
1
2
3
4
5
6
7
8
9

Fig. 3

Fig. 4

Capítulo 2

Crypsis of females and egg sacs in *Uloborus* sp. (Araneae, Uloboridae): a perspective from natural enemies’ vision

Crypsis of females and egg sacs in *Uloborus* sp. (Araneae, Uloboridae): a perspective from natural enemies' vision

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Abstract. The background-matching happens when an animal has a strong visual resemblance to the background, considering its color and body's pattern. Advanced visual models have permitted to consider the reflectance of organisms to estimate how predators can see and can differentiate the colors of their potencial prey items. Some spiders, in addition to present color patterns apparently very similar to the background, build structures, such as stabilimenta and/or egg sacs which may reduce the ability of predators to identify the visual contour of the spider body. In this study we investigate whether Hymenoptera and birds are able to distinguish color of an uloborid spider, its egg sac and the branches where the web is fixed, using chromatic and achromatic contrasts. We found that both groups cannot distinguish spiders to egg sacs and also egg sacs to branches by the chromatic contrast. We conclude that the coloration's pattern and the alignment position of spiders and their egg sacs may be important features to avoid predation by visually oriented predators in *Uloborus* sp.

Keywords: Background-matching, camouflage, visual models, orb weaver spiders.

INTRODUCTION

The color pattern of a species may be involved in thermoregulation, communication and defense against visually oriented predators (Ruxton, Sherratt & Speed 2004). In this sense, morphological and behavioral adaptations involving species with colors that reduce the risk of detection and recognition by natural enemies or their prey (Stevens & Merilaita, 2009) have a crucial role in the fitness of prey and predators (Bartos, Szczepko & Stanska, 2013). To compare the color of orchids and their mimetic mantises, for example, O'Hanlon, Holwell and Herberstein (2014) observed that the color of both is indistinguishable by pollinating bees, and this similarity in coloration increased significantly prey capture rate of mantis that lay in these flowers. Tso, Lin and Yang (2004) also compared the coloration of typical and melanic morphs of *Nephila pilipes* and also reported an increase in prey capture rate for typical morphs due to the numerous yellow bands distributed throughout the body, which reduces the conspicuity and the color contrast with the background vegetation.

An animal is background-matching when its coloration has a strong visual resemblance to the background, considering coloration and body pattern (Stobbe, Dimitrova, Merilaita & Schaefer, 2009). Therefore, camouflage patterns can be measured by the efficiency of an animal to represent a random sample of the background vegetation where it stays (Endler, 1978; Endler, 1984), but to obtain accurate measurements, it is necessary to quantify the energy reflected from an object in different wavelengths (Bennett & Théry, 2007; Eaton & Lanyon, 2003) and consider predators visual systems. However, the role of color from the perspective of natural enemies, in natural conditions, have received little attention (Stevens & Merilaita, 2009).

In addition, it is also important to consider that some organisms have the ability to combine the cryptic coloration with some postures and behaviors that increase camouflage efficiency, making them less conspicuous. This is defined as postural camouflage (Barbosa, Mäthger, & Hanlon, 2011). In spiders, two ways of protective body modifications were recorded: the first occur when the individual, through changes in color, in its shape or both, acquires colors similar to plants or inorganic objects; and second, when the spider mimics unpalatable individuals or acquires unpalatable structures (Peckham, 1889). Some species of the genera *Miagrammopes* and *Uloborus* (Uloboridae), for example, have long and slender legs and colors that resembles branches (Cushing, 1989; Lubin, Eberhard & Montgomery, 1978; Lubin, 1986; Opell & Eberhard, 1984; Opell, 1986), while some representatives of the genus *Wagneriana* (Araneidae) have a similarity to debris (Robinson & Robinson, 1970).

The evolution of these complex defensive behaviors in spiders can be attributed to their high number of natural enemies (Gonzaga, 2007). Thus, many animal groups can be pointed out as generalist spider predators, such as birds (Gunnarsson, 2007; L. Naef-Daenzer, B. Naef-Daenzer & Nager, 2000), hymenopterans (Blackledge & Pickett, 2000; Eberhard, 2001), lizards (Spiller & Schoener, 1998), ants and other spiders (Henschel, 1998). In birds, the hummingbirds are one of the most important predators of spiders, because they have to supplement their diet of nectar with proteins acquired from spiders and insects before the reproductive period (Pyke, 1980). Other important predators and parasitoids include several families of hymenopterans. The activity of these natural enemies can greatly affect the reproductive success of females (Smith, 1997). Peaslee and Peek (1983), for example, showed that 78% of egg sacs of *Octonoba octonarius* (Muma) (Uloboridae) were attacked by *Arachnopteromalus dasys* (Gordh) in the field.

From this, numerous advances in understanding the perception and processing of color in many animal groups have permitted to consider the reflectance of organisms using visual models that estimate how they (usually predators, prey or pollinators) see and how they can differentiate colors (Chittka, 1992; Goldsmith, 1990; Kelber, Vorobyev & Osorio, 2003; Stuart-Fox, Moussalli & Whiting, 2003; Tovee, 1995; Vorobyev & Osorio, 1998; Vorobyev, Osorio, Bennett, Marshall & Cuthill, 1998). In spiders, visual models that measure the reflectance of the body or decorations on the webs from Hymenoptera view spectrum and birds have been widely used (Bruce, Heiling & Herberstein 2005; Chittka, 2001; Rao, Webster, Heiling, Bruce & Herberstein, 2009; Tan & Li, 2009; Tan, et al., 2010; Théry & Casas, 2002; Théry, 2007; Tso et al., 2004) since these groups are seen as important natural enemies.

The aim of this study is to determine whether, considering the Hymenoptera and birds vision spectrum, there are differences in color of spiders, egg sacs and branches where *Uloborus* sp. web is fixed. We hypothesized that coloration of spiders, egg sacs and branches are very similar, making it difficult the viewing by visually oriented predators when foraging, acting on the spider eggs protection against natural enemies. Similarly, Cushing (1988, 1989) suggested that the alignment between female and its egg sacs in *Uloborus glomosus* makes both similar to a stick, and that this position is important to protect them against predation.

METHODS

Study area

Spiders were collected in November 2014 in a *Eucalyptus* plantation in Fazenda Nova Monte Carmelo, property of Duratex S.A. (18°45'11"S, 47°51'28" W), Estrela do

Sul, Minas Gerais, Brazil. Areas covered by *Eucalyptus* are interspersed with fragments of native savannas (Cerrado) in Fazenda Nova Monte Carmelo, but *Uloborus* sp. webs are constructed especially in the lower stratus of *Eucalyptus* branches, close to the layer of litter (0-50cm).

The study site has about 280 species of birds, of varying sizes and presenting different feeding habits. More than 40 of them are classified as insectivorous, and these, 12 are hummingbirds, the main avian predator of spiders.

Study species

The genus *Uloborus* belongs to Uloboridae family, which venom glands are completely reduced (Nentwig & Kuhn-Nentwig, 2013) and it spins a cribellar thread (Opell, 2013). The genus is currently composed of 80 species and only four of them are registered in Brazil - *U. ater* Mello-Leitão,1917, *U. minutus* Mello-Leitão 1915, *U. niger* Mello-Leitão 1917 and *U. tetramaculatus* Mello-Leitão 1940. The female of *Uloborus* sp. stays in resting position with the first two pairs of legs stretched in front of her body, and the egg sacs remains situated always in an adjacent position to the spider's body, also elongated, composing an appearance similar to a branch (Figure 1).

Collecting, processing and analyzing spectral data

To analyze the color of spiders and egg sacs, considering hymenopterans and birds vision spectrum, we collected 37 spiders with egg sacs and 37 branches of the trees where the webs were built. Additionally, we collected 205 leaves from the superior litterlayer to compose the background vegetation analyzed. We took the material to the laboratory and placed the samples under a black background, where we measured the percentage of reflectance of spiders, egg sacs and branches with the spectrophotometer Jaz (Ocean Optics, Inc.) and the SpectraSuite software. Before the measurements, we calibrated the spectrophotometer with standard color measurement (white and black). Then, we selected the reflectance data in a range of 300 to 700 nanometers (nm), considering the scope of the Hymenoptera and birds vision spectrum. We made the measurements using an interval of l nm to Hymenoptera nm and 0.3 nm for birds, constituting a sum of 400 and 1130 measurements for each group, respectively.

The coloration analysis of spiders, egg sacs and branches from Hymenoptera vision spectrum was performed in two steps. At first, we calculated the photoreceptors excitation values in the range of ultraviolet, blue, and green, under standard lighting conditions for day (D65) and background color (reflectance of leaves) from the color space displayed by bees with the software Photoreceptor Excitation. The spectral sensitivities of bees were used as a model because it is similar to those of wasps (Chittka, 1992), potential predators and parasitoids of Uloborus sp. The second step was constituted of hexagon and Cartesian plane building (Chittka, 1992), where we plotted the excitation levels of the three photoreceptors for spiders, twigs and egg sacs with the data of the Hymenoptera spectrum. Then, we added an achromatic central point, in which excitation of the three photoreceptors are equal, and the color contrast with the background can be considered null. Later, we calculated the Euclidean distance between the representative points of egg sacs, spiders and branches by chromatic and achromatic contrasts. This distance can be regarded as the contrast color of an organism within the color space (Nentwig, 2013). There is a threshold which the Hymenoptera are able to distinguish the colors, corresponding to 0.09 units of hexagon (uh) (Dyer, 2006). To obtain this distances, we calculated x and y values of photoreceptors excitations for spiders, egg sacs, and branches. We based the calculations on the following equations:

$$y = E(B) - 0{,}5 * (E(U) + E(G))$$

$$x = \sqrt{3}/2 * (E(G) - E(U))$$

where E is the excitation values for the photoreceptor UV (ultraviolet), B (blue) and G (green). Subsequently, we constructed a distance matrix using the package "ggplot2" (Wickham, 2009) in the R software (R Development Core Team, 2011). So, we compared the results between each group using chromatic and achromatic contrasts with the threshold value of 0.09 uh using a t-test in R software, with the package "stats" (R Development Core Team, 2011).

The coloration analysis of birds vision spectrum was performed with the software R (R Development Core Team, 2011) with the package "Pavo" (Maia, Eliason, Bitton, Doucet & Shawkey, 2013) and it is based on a three dimensional model comprehending tetrachromacy, in the shape of tetrahedron, where each edge of the polygon represents a photoreceptor excitation, which can be ultraviolet, blue, green and red. For this, we entered the reflectance data into the model and after we calculated the color contrasts of spiders, egg sacs and branches from the bird vision spectrum through the function "vismodel". Then, we added in the model the illumination pattern data for day (D65), and the reflectance values of the background vegetation. Finally, we plotted all points in tetrahedron color space and we also calculate the Euclidian distance between points.

Birds have five types of cone photoreceptor: four single cones and a double cone (Bowmaker, Heath, Wilkie & Hunt, 1997). So, the chromatic color contrast is represented by the relative excitation of single photoreceptors, and thereby determining color vision. On the other hand, the achromatic contrast is defined by excitation of double cone and has an important role in distinguish objects' texture (Jones & Osorio, 2004; Osorio, Vorobyev & Jones, 1999). We calculated both, chromatic and achromatic contrasts, between points expressed by egg sacs, spiders and branches by Euclidean distance (Théry & Casas, 2002) using the "coldist" function. The values were compared with the color birds discrimination threshold, which corresponds to 3 JND (Just Noticeable Distance) (Vorobyev & Osorio, 1998), using t-test with the package "stats". in R software (R Development Core Team, 2011).

RESULTS

Through the color measurements in spiders, egg sacs, and branches, it was possible to see a similarity in the three reflectance curves measured, with a low reflectance in the initial wavelengths (UV wave band), and increasing gradually as the wavelength is increased, with a peak of reflectance between 600 and 700 nm, corresponding to reddish colors in spectrum (Figure 2). It is also noticed that the standard reflectance curve of both spiders and egg sacs showed a considerable overlap, while the curve obtained by the branches showed a peak reflectance slightly lower.

The points represented for spiders, egg sacs and branches showed a cluster around the achromatic central point within both the hexagonal color space and Cartesian plane (Figure 3). The Euclidean distance between points denoted that spiders and egg sacs do not show significant difference considering the discrimination threshold of Hymenoptera ($t = -0.83$, $df = 36$, $p = 0.41$), whereas egg sacs and branches was even lower ($t = - 2.73$, $df = 36$, $p <0.01$) and spiders and branches showed chromatic contrast values exceeding the discrimination threshold ($t = 4.31$, $df = 36$, $p <0.01$) (Figure 4).

The distribution of points in the tetrahedral color space considering bird's vision spectrum also showed an aggregation including spiders, branches and egg sacs, denoting a deviation towards the red photoreceptor and occupying a color space a little distant from the central point (Figure 5). By the calculation of chromatic contrast against background vegetation, it was revealed that the average of points compared was below of discrimination’s threshold by birds (Figure 6). Thus, there is no significant difference between spiders and egg sacs (t = -38.99, df = 1368, p <0.01), spiders and branches (t = -8.82, df = 1368, p <0.01), egg sacs and branches (t = -27.16, df = 1368, p <0.01) by birds when they use all the photoreceptors. However, all of these comparisons were above the discrimination’s threshold by birds when considering the achromatic contrast (Figure 6). Therefore, by using only two photoreceptors to distinguish objects, the birds are able to differentiate spiders and egg sacs (t = 17.10, df = 1368, p <0.01), spiders and branches (t = 42.48, df = 1368, p <0.01), and branches egg sacs (t = 46.82, df = 1368, p <0.01).

DISCUSSION

The points in the hexagonal color space and the values obtained by the color contrast showed that Hymenoptera are not able to distinguish colors between spiders and egg sacs, and between egg sacs and branches. On the other hand, a greater distance between the points represented by spiders and branches highlighted that by hymenopteran insects can differentiate the colors of both. Similarly, our results showed that birds are also unable to discriminate between colors of spiders, egg sacs and branches. However, when it comes to the achromatic contrast, we conclude that

Hymenoptera and birds have a capacity for discernment between the three measured objects.

The achromatic contrast in Hymenoptera is related to stimulation of green photoreceptors and it acts to detect objects at long distance. Thus, the predator located the prey at a long distance, and when it approaches, there is a change to chromatic channel within short distance, changing the object identification process (Giurfa, Vorobyev, Kevan & Menzel, 1996). However, when the female and egg sacs of *Uloborus* sp. are seen in a long distance by Hymenoptera predators, the body outline is broken due the alignment, and it can confuse the predator, making difficult the identification of both as a possible prey. Similarly, Tso et al. (2004) observed that yellow bands, in contrast to the darker parts of the body *Nephila pilipes*, were important in breaking the spider body contour, so making difficult the identification of spider as a predator by Hymenoptera. Similarly, the linear stabilimenta of *Cyclosa mulmeinensis* composed of silk and detritus is important to distract predators, directing the attacks on decoration and consequently decreasing the efficiency of predators in capturing the spiders (Tseng & Tso, 2009). Despite the difficulty of detection *Uloborus* sp. through visual spectrum, Hymenoptera predators and parasitoids can also use a series of chemical signals to find their prey (Lewis & Tumlinson, 1988). Thus, it is possible that the predator may combine visual and chemical cues in order to achieve a greater efficiency in the capture of cryptic prey.

The alignment position of spiders and egg sacs also seems to play an important role in avoid detection by birds. Within this group, the achromatic signal is provided by excitation of double cone and it is important to the identification of the shape of objects (Jones & Osorio, 2004; Osorio, Vorobyev & Jones, 1999). When searching for prey with quite similar to background aspect where they live, birds use the achromatic signal to detect cues to allow the encounter of these prey (Osorio, Miklósi & Gonda, 1999; Stobbe et al., 2009). By this signs, some birds are able to analyze the shadows of objects, and also body discontinuity through the object's outline analysis (Stobbe et al., 2009), characteristics that appear to be essential to discern prey with cryptic appearance. The position occupied by the spider, always contiguous with its egg sac, however, may constitute a sign very difficult to be quickly analyzed and identified at relatively large distances may confuse these predators

Although seems hard to detect spiders and egg sacs as prey by the chromatic and achromatic signals, birds also can use the location of webs in the vegetation as a cue to localize easily the spider prey (Gunnarsson, 2007). However, the web detection by birds depends of the size, the amount of threads and web position in vegetation. In *Uloborus* sp., the web built during the maternal care period is smaller, has a smaller amount of threads and does not contain spiral turns, making its location very difficult (see Chapter 1).

In general, it was observed that the camouflage efficiency of *Uloborus* sp., is enhanced by the similarity of color between spiders and egg sacs and also by the body alignment with this structure. Many studies suggest that a strong similarity of geometric and illumination patterns are essential to maintain the effectiveness of color patterns observed in cryptic species (Merilaita, Lyytinen & Mappes, 2001; Stevens, Cuthill, Windsor & Walker, 2006). Then, the color and the alignment position of *Uloborus* sp. appears to support the crypsis hypothesis proposed in this study, and both must be combined to maximize the efficiency of avoiding predators.

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FIGURE CAPTIONS

Figure 1: A. Female of *Uloborus* sp. in its typical position. B, C. Female guarding its egg sac of *Uloborus* sp. D. Branches where *Uloborus* sp. built its webs in study site.

Figure 2: Reflectance percentage (mean and standard deviation) for spiders (green), egg sacs (blue) and branches (red).

Figure 3: A. Cartesian plane including reflectance of spiders, egg sacs and branches by Hymenoptera vision spectrum. B. Hexagon representing the excitation relative to the photoreceptors green, blue and UV, according to Hymenoptera vision spectrum.

Figure 4: Chromatic and achromatic contrasts relative to spiders, egg sacs and brunches by the Hymenoptera spectrum. The dotted line represents the discrimination threshold by Hymenoptera.

Figure 5: Distribution of points relative to spiders, egg sacs and branches from the bird vision spectrum on tetrahedron color space from different angles. The gray color point represents the achromatic central point, whose color contrast is null.

Figure 6: Chromatic and achromatic contrasts relative to spiders, egg sacs and brunches by the bird’s spectrum. The dark gray bars represents the chromatic contrast, light gray bars represents the achromatic contrast, and the dotted line represents the discrimination threshold by birds.

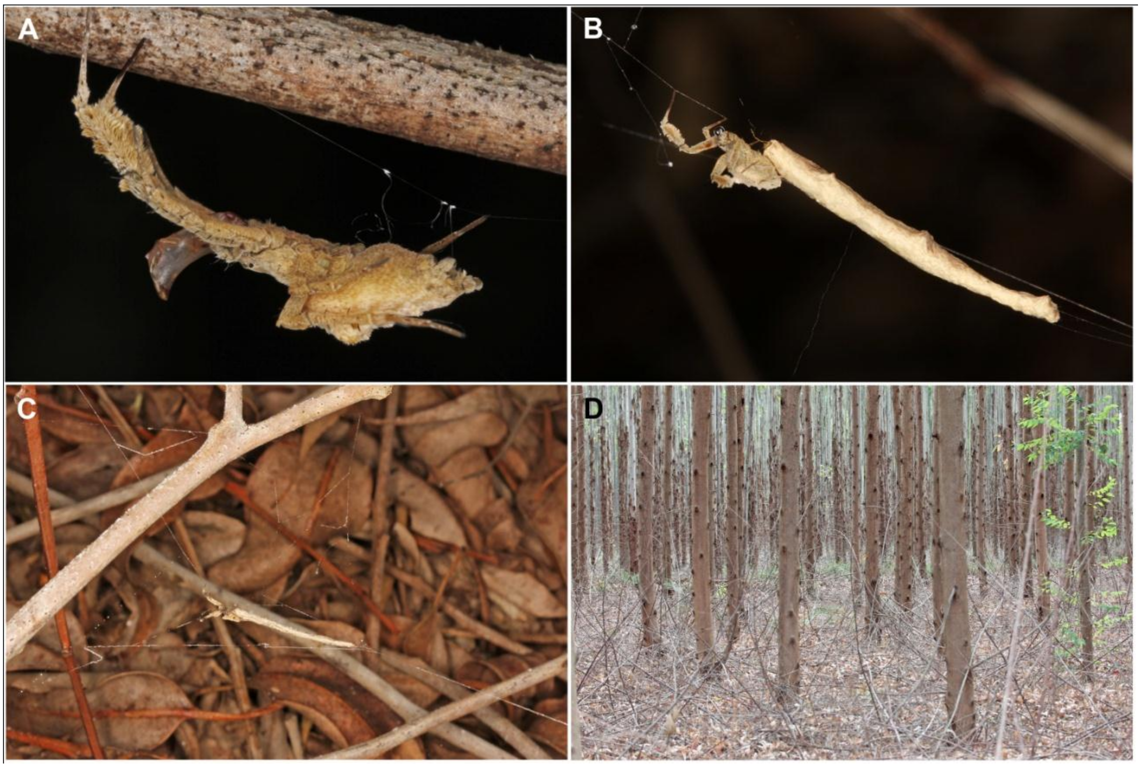

Figure 1

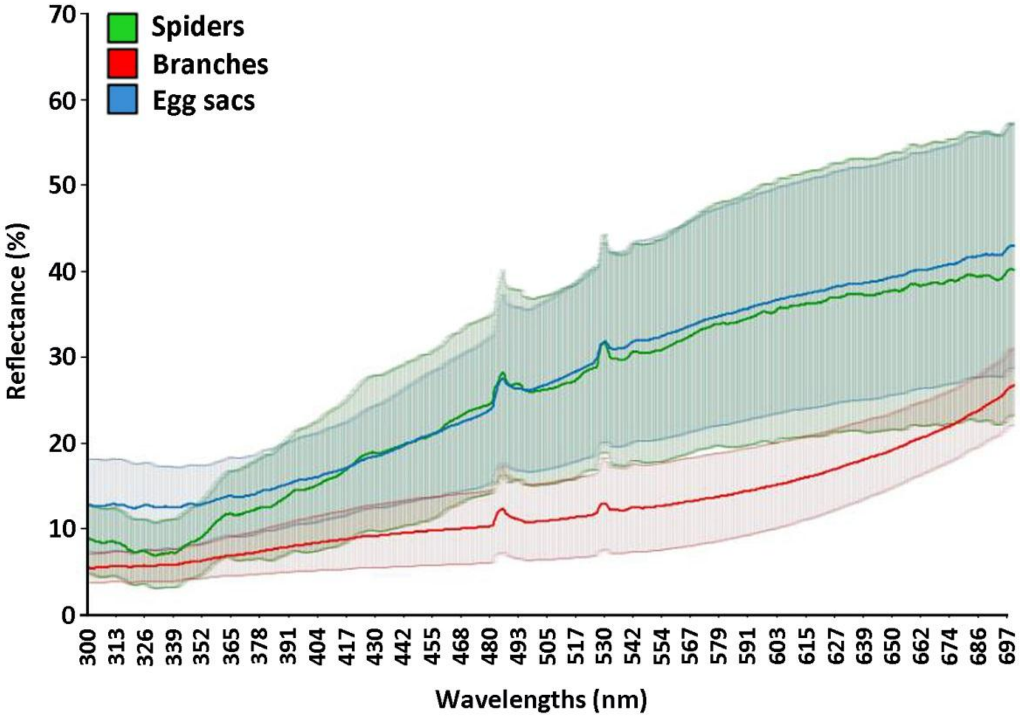
Spiders
Branches
Egg sacs
Reflectance (%)
0
10
20
30
40
50
60
70
300
313
326
339
352
365
378
391
404
417
430
442
455
468
480
493
505
517
530
542
554
567
579
591
603
615
627
639
650
662
674
686
697
Wavelengths (nm)

Figure 2

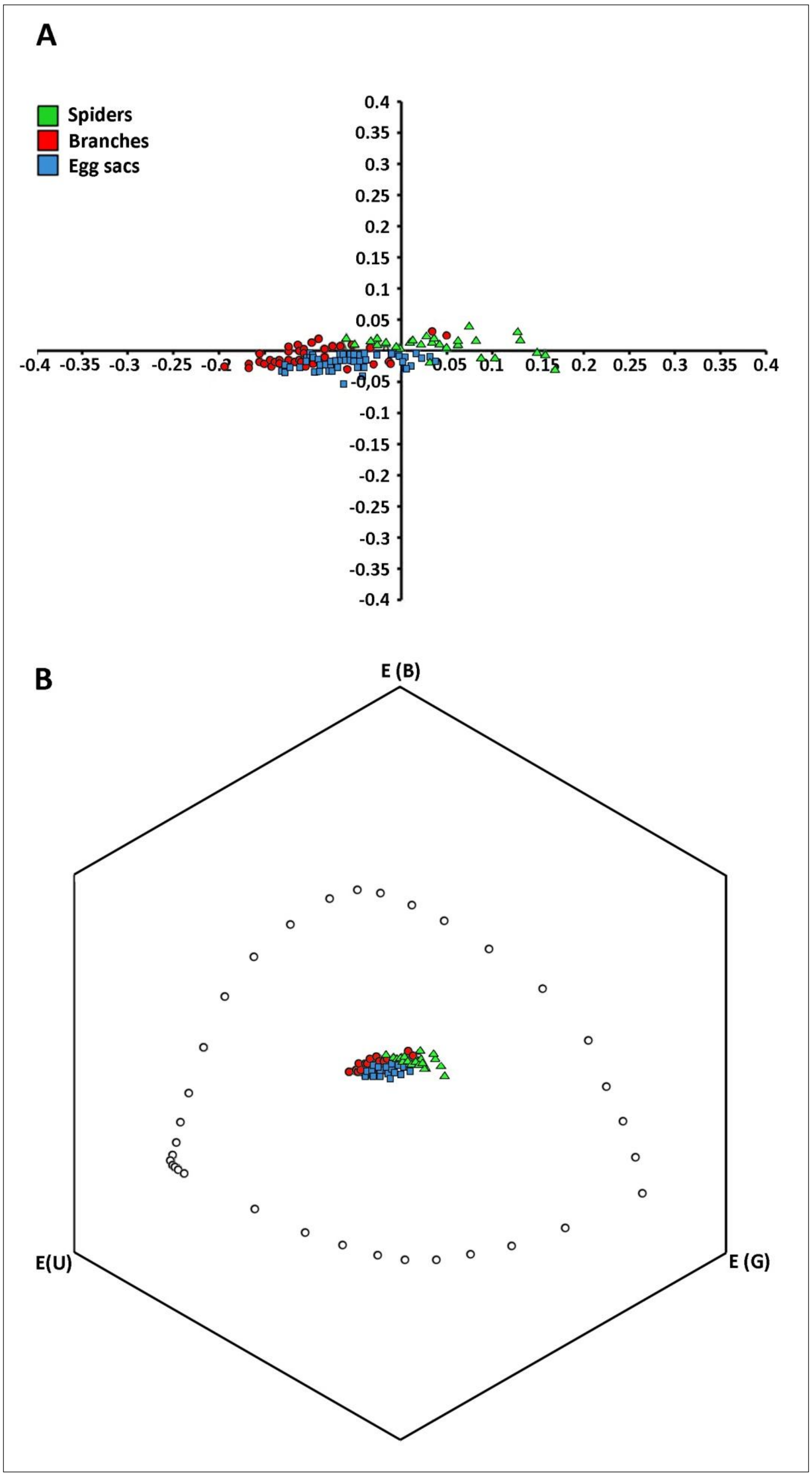
A
Spiders
Branches
Egg sacs
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
-0.05
-0.1
-0.15
-0.2
-0.25
-0.3
-0.35
-0.4
-0.4 -0.35 -0.3 -0.25 -0.2 0.05 0.1 0.15 0.2 0.25 0.3 0.35 0.4
B
E (B)
E(U)
E (G)

Figure 3

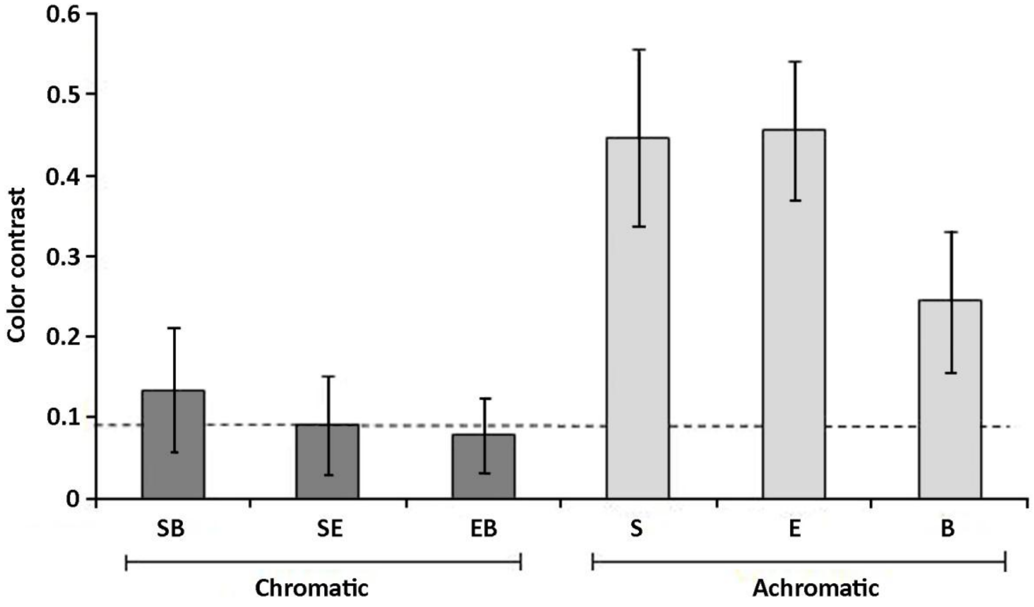
0.6
0.5
0.4
0.3
0.2
0.1
0
Color contrast
SB
SE
EB
S
E
B
Chromatic
Achromatic

Figure 4

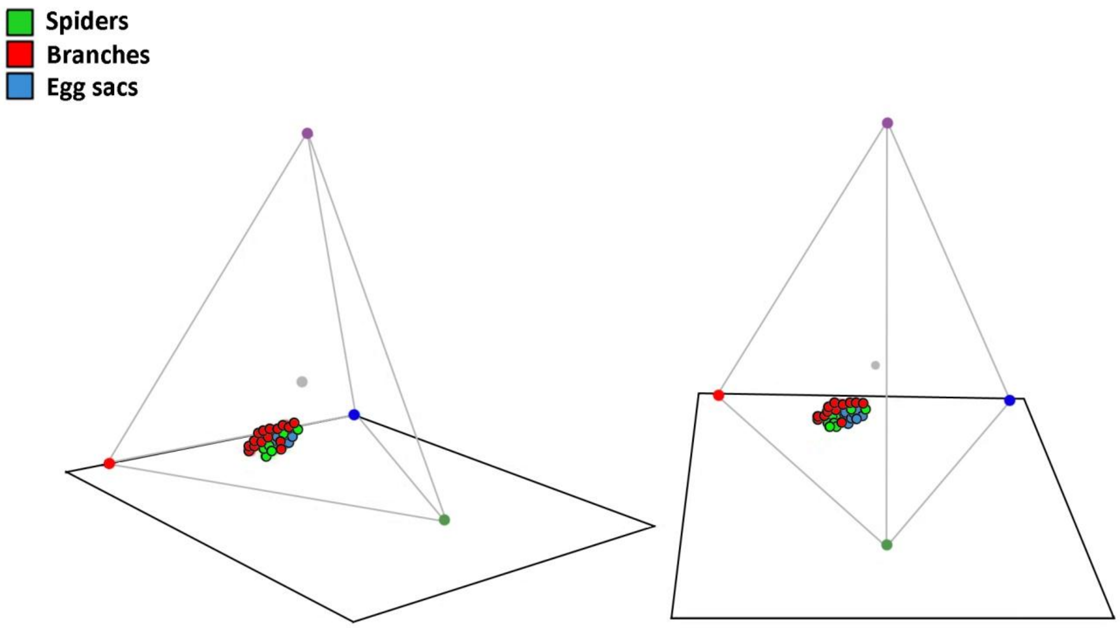

Figure 5

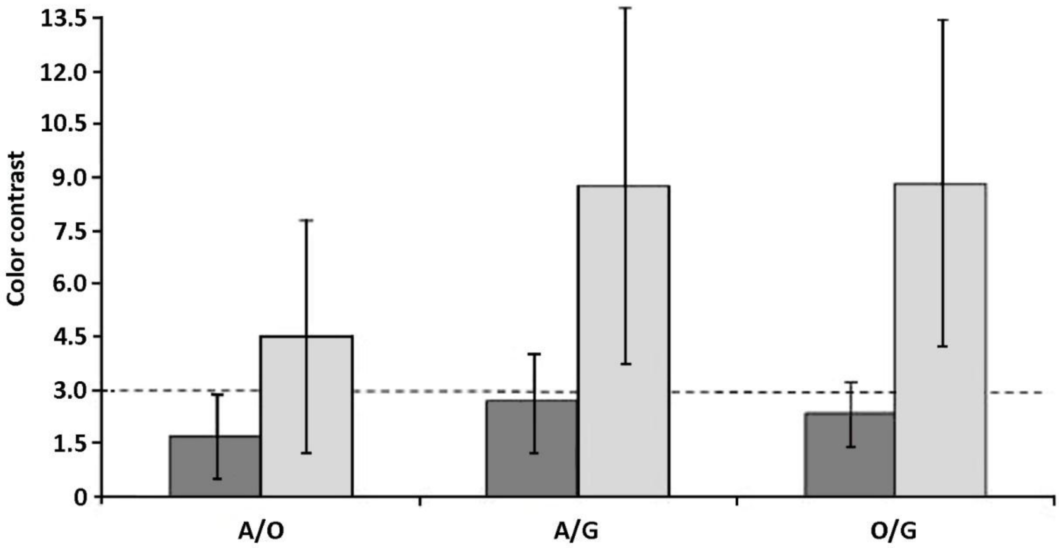

Figura 6

CONSIDERAÇÕES FINAIS

A partir desse trabalho foi possível concluir que *Uloborus* sp. apresenta grande investimento no cuidado maternal na fase de proteção aos ovos, permanecendo em teias que não permitem a captura de presas e reagindo agressivamente contra quaisquer possíveis agentes que possam representar riscos para suas ninhadas. A intensidade dessas reações agressivas independe do tamanho da ninhada e do tamanho corporal da fêmea, indicando que (1) a proteção deve ser muito importante para assegurar o sucesso da ninhada, (2) todo o esforço reprodutivo das fêmeas deve ser direcionado para uma única ooteca, (3) mesmo fêmeas pequenas devem apresentar maior sucesso reprodutivo investindo toda sua energia remanescente após a produção dos ovos em protegê-los. Entretanto, a baixa frequência observada de predadores de ovos atacando as ootecas pode indicar a eficiência desses comportamentos na proteção dos filhotes contra predação, o que justificaria o elevado investimento energético da mãe no período de cuidado com os filhotes. Além disso, a dificuldade de detecção da aranha e sua ooteca por predadores visualmente orientados possivelmente constitui outro fator importante para minimizar o risco de predação de adultos e ootecas. Permanecendo em uma posição críptica, alinhada com suas ootecas, as aranhas podem ser confundidas com gravetos presentes em abundância no ambiente que ocupam e, assim, diminuiriam as chances de serem identificadas por aves e vespas predadores que estivessem procurando por presas com o formato corporal de uma aranha.