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Notes on the behavior of the kleptoparasitic spider *Argyrodes elevatus* (Theridiidae, Araneae)[1]

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Kleptoparasitism is an interaction in which one individual steals captured or processed food from another; spiders of the subfamily Argyrodinae (Theridiidae) may present kleptoparasitic behavior. Aiming to increase the knowledge about this unique strategy, we describe activities accomplished by the kleptoparasitic spider *Argyrodes elevatus* (Theridiidae) in webs of captive host spiders. After a prey was captured by the host spider, a second prey was offered, so that the kleptoparasite could steal the first prey while the host spider was immobilizing the second one. Using this method, we were able to see a wide range of events, such as the theft of stored preys, the sharing of a prey with the host, the theft of the egg sacs, the predation of host spiders, and others. Finally, we discuss how kleptoparasitism could vary in function of host behavior and how the high behavioral variability of *Argyrodes elevatus* could be explained.

Keywords: kleptoparasitism, behavior, *Argyrodes elevatus*, Argyrodinae, Theridiidae.

Notas sobre o comportamento da aranha cleptoparasita Argyrodes elevatus *(Theridiidae, Araneae).*
O *Cleptoparasitismo* é um tipo de interação na qual um indivíduo rouba ou furta alimento adquirido por outro; aranhas da subfamília Argyrodinae (Theridiidae) podem apresentar esta estratégia. A fim de ampliar o conhecimento acerca deste curioso comportamento, descrevemos aqui as atividades empenhadas pela aranha cleptoparasita *Argyrodes elevatus* (Theridiidae) em teias de aranhas hospedeiras, em laboratório. Após a captura de presa por parte da aranha hospedeira, uma segunda presa era oferecida, de maneira que o cleptoparasita pudesse furtar a primeira enquanto a hospedeira capturava a segunda. Através deste método, observamos uma grande variedade de eventos, tais quais: furto e compartilhamento de presas capturadas, furto de ooteca e predação da aranha hospedeira, entre outros. Por fim, discutimos a flexibilidade do cleptoparasitismo em função do comportamento da aranha hospedeira e como pode ser explicada a alta variabilidade comportamental de *Argyrodes elevatus*.

Palavras-chave: cleptoparasitismo, comportamento, *Argyrodes elevatus*, Argyrodinae, Theridiidae.

Introduction

Kleptoparasitism is a term that refers to a reciprocal interaction in which one individual takes advantage from the foraging investments of another. Kleptoparasitic behavior occurs on a diverse array of taxa, including cnidarians, annelids, arthropods, mollusks, echinoderms, fishes, reptiles, birds and mammals (Iyengar, 2008); in this wide range, the host-parasite interactions vary strongly.

Some researchers have been compiling features of this kind of behavior to find a single and clear definition encompassing every reciprocal action in which one individual takes advantage from the foraging investments of another (Brockmann & Barnard, 1979; Morand-Ferron, Sol & Lefebvre, 2007; Ivengar, 2008). We could resume the situation saying that kleptoparasitism is a plural strategy, that there are different kinds of it, and consider kleptoparasitism as the action of robbing or stealing (*kleptein*, from the greek: to steal), as used to describe inter and intraspecific interactions in which an animal takes food resources from a host (Crespi & Abbot, 1999). The literature also presents expressions such as "piracy", "robbing" or "stealing", but these words may carry anthropomorphic connotations (Giraldeau & Caraco, 2000), so that we will prefer the term kleptoparasitism.

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Kinds of kleptoparasitism

Giraldeau and Caraco (2000) sustain that there are three different kinds of kleptoparasitism: (i) *aggressive*, if it is accomplished with threat or aggression; (ii) *scramble*, if the food item is simultaneously exploited by the host and one or more kleptoparasites with little or no aggressive behavior, and (iii) *stealth*, when the kleptoparasite take the food away avoiding to be perceived by the host.

Some interactions, which are also called kleptoparasitism, do not fit in the classification presented by Giraldeau and Caraco (2000). Cleptoparasitic bees (written with "c" in the literature), also called *cuckoo-bees* (e.g.: Bogusch, Kratochvíl & Straka, 2006), do not steal food items from their hosts, but lay their eggs in nests of others bees, and their larvae are born before the larvae of the host. The invader larva eats the provision stored in the nest and preys on the eggs of the host (Rozen Jr., 1991). The behavior of cleptoparasitic bees resembles the behavior of parasitoid organisms (Allaby, 1994), as, for example, of flies of the family Bombyliidae (Yeates & Greathead, 1997).

The anthropomorphic terms "steal" or "rob" are used to describe the more aggressive behaviors of some bees that take their provisions of nectar and pollen from the nests of other species. After that, these bees kill both adults and larvae and can, in a single attack, eliminate the nest of the "host" species. Bees that attack other colonies in this manner are called *robber bees* (Free, 1955; Sakagami, Roubik & Zucchi, 1993) or *cleptobiotic bees* (Pompeu & Silveira, 2005; Marchi & Melo, 2006). This kind of attack behavior is also accomplished by ants and, in this case, the interaction is termed *cleptobiosis* (Richard, Dejean & Lachaud, 2004).

Kleptoparasitism in spiders

At least 11 spider families have species that scrounge the food captured by others species: Oonopidae (Bristowe, 1958 apud Kaston, 1965), Dictynidae (Griswold & Meikle-Griswold, 1987), Uloboridae (Struhsaker, 1969), Symphytognathidae (Vollrath, 1978), Anapidae (Ramirez & Platnick, 1999), Mysmenidae (Coyle & Meigs, 1989; Coyle, O'Shields & Perlmutter, 1991), Sparassidae (Jackson, 1987), Eresidae (Wickler & Seibt 1988), Salticidae (Jackson & Blest, 1982; Jackson, 1985), Oxyopidae (Gonzaga, Santos & Dutra, 1998) and Theridiidae (Robinson & Robinson, 1973; Vollrath, 1979). Spiders of the genera *Olios* (Sparassidae), *Stegodyphus* (Eresidae), *Portia* and *Simaetha* (Salticidae) use the aggressive kleptoparasitism to remove the prey from their hosts (Jackson, 1987; Wickler & Seibt 1988; Jackson & Blest, 1982; Jackson, 1985). All the others spiders (except theridiids) merely cohabit webs or share food with their hosts.

Theridiidae is the family with more kleptoparasitic species (Elgar, 1993), all of them within the subfamily *Argyrodinae* (Agnarsson, 2002; Gonzaga, 2007). Inside this subfamily we could find a great variety of *kleptoparasitic* behaviors. Some species, for example, of the genus Argyrodes, can perform the three kinds of kleptoparasitism pointed out by Giraldeau and Caraco (2000): they can feed with the host spider (Robinson & Robinson, 1973), or remove surreptitiously the preys from the host web (Vollrath, 1979; Whitehouse, 1986; Cangialosi, 1990; 1991), or even use aggressive behavior in order to take away the prey from the host (Cangialosi, 1997). Furthermore, argyrodinae kleptoparasites can eat silk from the host web (Higgins & Buskirk, 1998; Tso & Severinghaus, 1998; Miyashita, Maezono & Shimazaki, 2004), catch rejected or undetected preys (Rypstra, 1981; Grostal & Walter, 1997) and even prey onto the host spider (Whitehouse, 1987; Cangialosi, 1997).

Although some studies have dealt with the evolution and diversity of kleptoparasitism in Argyrodinae (Whitehouse et al. 2002; Agnarsson, 2004), the knowledge about this foraging strategy among these spiders is clearly insufficient when we consider the wide variability within the group. We think the lack of knowledge in this issue occurs, in part, because the literature misses much of the natural history data about the species[1].

In this way, we present here descriptions of some events that occurred during foraging activity of the kleptoparasite *Argyrodes elevatus* (Taczanowski, 1873) in many distinct host webs. We were able to see a wide range of behaviors, which

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[1] Dr. César Ades was very enthusiastic about natural history data. One of his dreams was to write a book about the spiders of the campus (at the University of São Paulo), with many beautiful spider and web photographs, side by side with field notes about each species. In a very direct way, this paper is a grandchild of César's contagious enthusiasm that infected a new generation (MCS) through an intermediate one (HFJ). And so they go, all these scientific children, spreading the ideals of an old and beloved master.

include the theft of prey items, aggressive kleptoparasitism, the sharing of a prey with the host, the theft of egg sacs, the predation of juvenile and adult host spiders (araneophagy) and the capture of preys using the host web – without any participation of the host spider.

Methods

Collection and maintenance

A. elevatus specimens were collected in urban forests, in the area of Instituto Butantan and Cidade Universitária Armando Salles de Oliveira (USP's main campus, in the city of São Paulo), and around the buildings of these institutions. We have collected these kleptoparasites in webs of *Nephila clavipes*, *Nephilengys cruentata* (Fabricius, 1775) (Nephilidae) *Achaearanea tepidariorum* (Theridiidae), *Argiope argentata* (Fabricius, 1775), *Araneus bogotensis* (Keyserling, 1864), and *Araneus venatrix* (C. L. Koch, 1838) (Araneidae).

We observed the activities of *A. elevatus* in the laboratory for two years (from feb-2006 to mar-2008), totalizing more than 400 hours upon approximately 90 individuals, in webs of the hosts *A. tepidariorum*, *Latrodectus geometricus* (C. L. Koch, 1841) and *Latrodectus curacaviensis* (Müller, 1776) (Theridiidae). Some casual observations were accomplished in webs of *A. bogotensis* (n = 2), *A. venatrix* (n = 3) (Araneidae) and *Tidarren sysiphoides* (n = 1) (Walckenaer, 1842) (Theridiidae). The host species were collected in synanthropic areas in the city of São Paulo, except for *L. curacaviensis*, that were collected in Seropédica, Rio de Janeiro.

Host spiders were maintained individually in acrylic transparent cubic boxes (25 cm) with moist cotton and fed every 15 days with crickets (*Grillus* sp.) or beetle larvae (*Tenebrio molitor*). *A. elevatus* cannot survive more than four days in solitary, individual boxes, so we maintained them in the web of *L. geometricus*. Since *A. elevatus* cannot steal preys from these webs (MCS, personal observations), we could control her starvation period before the observational phase.

Triggering and observing the kleptoparasitism

In order to observe the foraging behavior, the kleptoparasite was placed into boxes where a host spider had constructed its capture web, and then we offered preys to the host. Prey items were attached onto the gumfoot lines of the theridiid webs or on the viscid spiral of the araneid orb webs. We introduced just one adult female *A. elevatus* in each host web, except during preliminary observations when we put together one male and one female (n = 8), two sub-adult females (n = 1) or three sub-adult females (n = 3). After the capture and storage of the first prey by the host spider, a second prey was offered so that the kleptoparasite could steal the first one (already wrapped and poisoned) while the host was immobilizing the second one. At each return of the host to the hub, we offered a new prey at the periphery of the host web. This procedure was repeated until we obtained a successful stealing bout.

Although most host spiders catch the prey immediately, sometimes we had to offer a second prey before it would go for the first one (when the first prey was ignored for ten minutes). We offered as prey cricket nymphs or beetle larvae, with size approximately equal to the body of the host spider (cefalothorax + abdomen), cricket nymphs with size equal to the kleptoparasite body (approximately 3 mm), and *Drosophila* flies.

Results

Mating and egg sac laying

Three sequences of courtship were observed when males and females were left in the host web: two in *A. tepidariorum* webs and one in *L. geometricus* web. The male approaches the female, vibrating and spinning his forelegs until he touches her with the tarsi; the female turns to the male and both, face to face, extend the first pair of legs over each other, with the ventral face of the abdomen pointed to the upper side of the web. This contact between male and female takes two minutes at most. In the meantime, the male "boxes" the female genital area with the pedipalpi, probably transferring sperm masses. The male then moves back one or two centimeters while the female stays in the same place and position. After a few seconds, the male approaches again and restarts the contact, touching her with the tarsi again. The complete mating is a repetition of numerous bouts like this one, totalizing more than an hour. During all the three observed matings, the host spiders did not react to the kleptoparasite's movements. One of these females laid an egg sac one day after mating.

A. elevatus may lay egg sacs on the host webs. Egg sacs were laid commonly at the periphery of the web, amidst a previously constructed, small thread structure. The kleptoparasite does not stay near the egg sac after laying it. Spiderlings emerged from four of the 21 egg sacs deposited by 18 of the captured females, but we were not able to maintain them alive beyond the third instar.

Responses towards the host

A. elevatus foraging activity starts when the host spider detects a prey. The kleptoparasite, in response to the movements generated in the host web, extends his first pair of legs and spin it repeatedly, in a very characteristic behavior called "rotary probe" (Whitehouse, 1986), until it grasps threads and moves towards the hub. During this locomotion, the kleptoparasite cuts off many host web threads and fix her own lines, always laying a dragline behind her path. *A. elevatus* varies its activity in function of the host spider behavior: it moves faster towards the prey stored at the hub when the host spider is wrapping a new prey at the periphery of the web, but moves slowly when the host arrives at the hub.

The kleptoparasite remains almost immobile when there is no prey on the web, and the host is in resting posture, at the hub. When put in a host web, it tends to go to the superior edges of the box, lay two or three threads onto the strand lines of the host web and stay motionless over these threads.

Hosts catch kleptoparasites

While walking on the web of the host, *A. elevatus* cuts original silk threads and replaces it with her own thinner threads, a behavior that probably reduces the chances of being detected by the host spider. Notwithstanding this behavior, the host occasionally perceives, run towards and even catches the kleptoparasite. When detected, the kleptoparasite interrupts the approach (towards the prey) and freezes. When chased, it quickly runs away through its dragline; it can also jump away from the web, if the host continues the attack.

Despite these evasive tactics, we could register *A. tepidariorum* capturing *A. elevatus* (n = 4); two of these instances were accomplished by the same host spider on distinct occasions. We also observed *Tidarren sisyphoides* (Theridiidae) catching *Argyrodes* sp. in the laboratory (n = 1), and *Nephila clavipes* (Nephilidae) cacthing *Argyrodes* sp. (probably A. elevatus) in the field (n = 1). *A. tepidariorum* and *T. sisyphoides* captured kleptoparasites by sticky silk wrapping. *N. clavipes* bit the kleptoparasite and started to ingest it simultaneously with an already subdued prey (which the kleptoparasite was attempting to reach).

Agonistic behavior towards the host

Although *A. elevatus* can sometimes be caught by host spiders, it may occasionally use an aggressive behavior towards the host. The kleptoparasite shakes intensively and repeatedly the web with its forelegs, while walking towards the hub of the web. In these circumstances, the host stays mostly motionless after the aggressive behavior. In one occasion, *A. elevatus* successfully dislodged a host (*L. curacaviensis*) that was finishing immobilizing a beetle larva, and went on to reach and steal the food.

In another occasion, *A. elevatus* walked towards the host spider *A. tepidariorum* while it was eating a cricket (of the same size of the spider's body). The host spider moved a few centimeters away and the kleptoparasite reached the cricket, but could not steal it before the return of the host, that chased away the kleptoparasite and got back the cricket.

Thefts of captured prey

We registered 23 well-succeeded thefts of previously captured and stored preys. These thefts occurred in webs of *A. tepidariorum* (n = 12), *L. curacaviensis* (n = 10) and *A. venatrix* (n = 1). Thefts were not observed in *L. geometricus* webs. We could see also unsuccessful bouts in webs of *A. tepidariorum* (n = 8), *L. curacaviensis* (n = 3) and *L. geometricus* (n = 5).

The kleptoparasite is able to steal food item once the host spider, after having captured, wrapped and brought the first prey to the hub, runs to catch the second offered prey. While the host spider is occupied immobilizing the second prey, the kleptoparasite approaches the stored prey, cuts threads around it and carries it attached on the spinnerets to the web periphery, where it fixes many threads connecting the stolen prey and two or three points on the host web. This behavior results in a rudimentary web – inside the host web – where the kleptoparasite feeds itself the stolen prey. Before starting the ingestion, *A. elevatus* strongly shook the web, as it was verifying if the host spider could or not detect and chase it to recover the stolen item. In fact, sometimes the host spider was able to perceive these vibrations, run forward the kleptoparasite and, by repelling him, retrieve the prey.

Feed with host

Although we have not observed thefts in *L. geometricus* webs, A. elevatus could once feed together with this host species. Feed with host also occurred in *A. tepidariorum* (n = 2; preys: beetle larvae and cricket sized equal host spider; Fig. 1) and *L. curacaviensis* webs (n = 2; preys: beetle larvae; Fig. 2). *A. elevatus* approaches the prey that is being ingested by the host, just like it approaches any stored prey. The food sharing can take from a few seconds to more than an hour, and it is eventually interrupted by movements of the host spider. The host often chases the kleptoparasite away; in these cases, the kleptoparasite runs away through its dragline.

In one event, *A. elevatus* stole the prey it was sharing with the host. *L. curacaviensis* perceived vibrations from another prey – that was wrapped but not deceased yet – and ran for it, then the kleptoparasite immediately started to cut threads around the prey that was being shared, and carried it to the periphery of the web.

Argyrodes elevatus *preys on the host spider* Araneus venatrix

In one occasion, *A. elevatus* bit a foreleg of *A. venatrix* (Araneidae). The host spider was an adult female that was neither molting nor recently molted. It was the only foraging event by *A. elevatus* that we could see in *A. venatrix* webs.

We offered crickets (approximately 8 mm) a few hours after we introduced *A. elevatus* (an adult female) in the orb web, just like we did in experiments with tridimensional webs. The kleptoparasite remained motionless on the edge of the web, while the host captured the prey and started to eat it at the hub. After five minutes, we offered a second cricket, but neither the kleptoparasite nor the host attempted to capture it. The kleptoparasite, instead, started to move towards the hub; in a few minutes, it was in the hub manipulating and biting the prey that the host was eating ("feed with host" behavior).

With his pedipalpi, chelicerae and first pair of legs, the kleptoparasite touched many times the tarsi of the host, while sharing the cricket. The host reacted aggressively to these contacts, shaking strongly the web and making sharp movements with its forelegs. These responses repelled the kleptoparasite about three centimeters away from the prey, but after a few seconds it returned to share the prey, and this cycle was repeated for more than four hours.

The next day (more than 14 hours after offering the first cricket), we found the kleptoparasite ingesting the deceased host spider, in the hub. The cricket was approximately ten centimeters away from the hub, probably transported by the kleptoparasite.

Unfortunately, we could not maintain *A. venatrix* in the laboratory to watch more events like this. During field observations, we found three times an individual *A. elevatus* feeding itself the deceased *Araneus* sp host (probably *A. venatrix*). In laboratory, we observed *A. elevatus* feeding itself the deceased hosts *L. geometricus* and *Araneus bogotensis* but, as in the field observations, we do not know why the host died neither how the kleptoparasite reached them.

Argyrodes elevatus *spiderlings prey on the host spider* Latrodectus curacaviensis

Approximately 30 *A. elevatus* spiderlings emerged from an egg sac that was laid on the periphery of a *L. curacaviensis* web. The host was in the web, but the adult kleptoparasite had been removed. The spiderlings remained near to the egg sac for 25 days, when we fed the host spider with a large beetle larva (15 mm). The vibrations caused by the host spider capturing the larva attracted the spiderlings. They approached the hub and, 20 minutes after the host had captured the prey, at least four spiderlings were touching the larva with their forelegs, pedipalpi and chelicerae. The spiderlings also touched the leg of the host, who walked four centimeters away from the prey. As more spiderlings approached the immobilized prey, two of them moved toward the host spider, touching it and even remained clinging for a while to its abdomen's surface. The only effective reaction of the host to the attack of the spiderlings was to groom itself for more than one hour: it left the prey, walked slowly away from the center of the web, and started to massage its legs on the chelicerae, and to pass its legs over its abdomen and spinnerets; the two

Figure 1: *Argyrodes elevatus* sharing prey with host spiders *Achaearanea tepidariorum*. Photos: M. C. Silveira; drawings: D. D. Guarda.

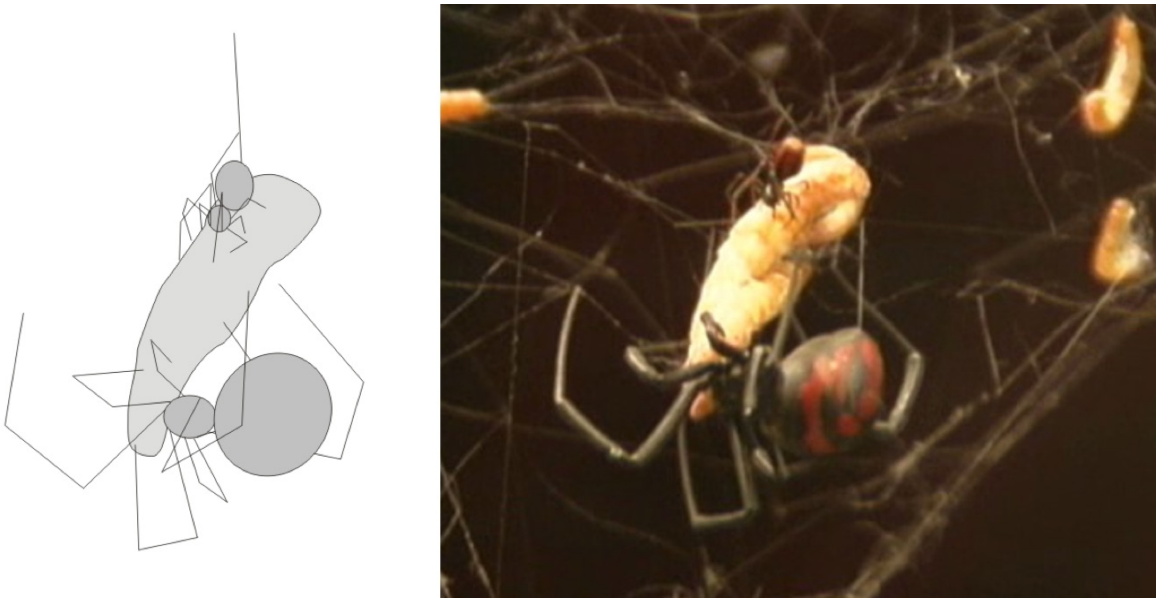

Figure 2: *Argyrodes elevatus* sharing prey with host spider *Latrodectus curacaviensis*. Photo: M. C. Silveira; drawing: D. D. Guarda.

spiderlings continued to pursue and touch it, while the others stuck to the larva.

The next morning, we encountered three *A. elevatus* spiderlings eating the deceased *L. geometricus*; eight of them were near the larva, and the rest (most) of them remained near the egg sac. The spiderlings near the host or the larva presented visibly turgid abdomens.

Live prey capture

A. elevatus living in host webs was able to capture prey by its own, wrapping it with silk while the host was immobile, or capturing another prey. We observed these predatory events in webs of *A. tepidariorum* (n = 5, preys: crickets with the size of the kleptoparasite body) and *L. geometricus* (n = 5; two crickets and three beetle larva with the size of the kleptoparasite body). In one case, differently from the others, *A. elevatus* did not start to eat the beetle larva right after immobilizing it. Instead, it cut threads around the prey, fixed a dragline to it and remained motionless for more than three hours. *A. elevatus* also caught *Drosophila* flies in *A. bogotensis* orb webs (n = 2), but in these cases the host spiders were not in the web.

Thefts of egg sacs

We registered four thefts of egg sacs, all of them in *A. tepidariorum* webs. These egg sacs did not seem functional: two of them were already emptied, one was laid by a virgin female and the other one was unconventionally disfigured. Despite this, the host spiders promptly protected these egg sacs. In one of these events, the host spider was able to recover the stolen egg sac (from which the spiderlings had emerged 9 days before), pursuing and chasing away the kleptoparasite.

Another egg sac theft was accomplished communally by a male and a female *Argyrodes* sp. (probably *A. elevatus*). While the host *A. tepidariorum* shook strongly the web with its forelegs directed to one kleptoparasite (which remained immobile), the other one approached the hub; this second kleptoparasite stopped moving when detected by the host, and then the first one – which was motionless – started to walk toward the hub (where the egg sac was deposited). This interchanging approach occurred until the female kleptoparasite reached the egg sac, cut threads around it and brought it to the periphery of the web. Then the male kleptoparasite followed the female and ate the stolen egg sac together with her. The host remained near the hub performing searches (plucking and tensing threads with the first pair of legs). This egg sac was also unconventionally disfigured, not at all like the normal spherical *A. tepidariorum* egg sacs.

Discussion

Kleptoparasite behavior varies in function of host spider behavior

Argyrodes kleptoparasites may be encountered in webs of many host spider species; these different webs may have very different structures: they are two- or tridimensional, with or without a closed hub. As expected, the kleptoparasite tactics can vary accordingly with the kind of web and host behavior. In our observations, there were host species who did not allow the theft of the prey, e.g. *Latrodectus geometricus.* In fact, there is no record in the literature of kleptoparasitism in *L. geometricus* webs. The only register of Argyrodinae in Latrodectus webs was made by Sierwald & Fenzl (1999), who observed the kleptoparasites *A. elevatus*, *Neospintharus furcatus* (O. P.-Cambridge, 1894) and *Faiditus caudatus* (Taczanowski, 1874) living in webs of *Latrodectus bishopi* (Kaston, 1938). However, we could observe thefts of captured preys in *L. curacaviensis* webs, despite the kleptoparasite *A. elevatus* not invading these webs in nature.

The host web structure may be related with the occurrence or non-occurrence of theft of prey by *A. elevatus. L. geometricus* webs have a peripheral hub (where the spider stores the caught preys), differently of *A. tepidariorum* webs (where the theft occurs), that have a central hub (Benjamin & Zschokke, 2003). The *L. curacaviensis* web is similar of *A. tepidariorum* web, with the hub on center of the 3D structure. We consider that difference in the hub position is related to the non-occurrence of theft of stored preys by *A. elevatus* in *L. geometricus* webs. Baba, Walter & Miyashita (2007) suggested that the presence or absence of a closed hub in the host web is the principal factor influencing the tactic used by *Argyrodes kumadai* (Chida & Tanikawa, 1999): in webs of host species *Agelena silvatica* (Oliger, 1983) (Agelenidae), the kleptoparasite only capture ignored or rejected preys, but in webs of *Cyrtophora moluccensis* (Doleschall, 1857) (Araneidae), which have no well-delimited hub, it can steal already immobilized preys.

Our data agree with the suggestion of Baba et al. (2007) that the hub position is crucial to the occurrence of thefts by kleptoparasites. But we cannot forget that there are many others factors that can influence the strategy of the kleptoparasite, as the kind of host web silk, that may be cribellated or ecribellated (Whitehouse, 1988); the aggressiveness of the host spider (Henaut, Delme, Legal & Williams, 2005); the relative abundance of each potential host species in a specific site (Cangialosi, 1997). Some factors intrinsic to the kleptoparasite may also interfere on the tactic choice, as starvation periods (Koh & Li, 2003).

Araneophagy

Catching adult host spiders is a common strategy used by Argyrodinae species of genera *Rhomphaea* (Whitehouse, 1987; Horton, 1983) *Ariamnes* (Eberhard, 1979) and *Neospintharus* (Wise, 1982; Cangialosi, 1997; Houser, Jennings & Jakob, 2005). The kleptoparasites *Argyrodes fissifrons* (O. P.-Cambridge, 1869) (Tanaka, 1984) and *A. antipodianus* (Whitehouse, 1986) can also catch their respective hosts *Agelena limbata* (Thorell, 1897) (Agelenidae) and *Achaearanea* sp. (Theridiidae), which are larger than them. However, these araneophagus Argyrodes only attack adults host when these hosts are on molt or recently molted and, therefore, more vulnerable.

We were able to see *A. elevatus* biting the host *A. venatrix* on its legs, and consequently killing it. The host spider was an adult female, larger than the kleptoparasite, and was not molting. This araneophagy event was not similar to the host predation accomplished by other Argyrodinae spiders. While *A. elevatus* bites the host – like other opportunist *Argyrodes* spiders (Tanaka, 1984; Whitehouse, 1986), either *Rhomphaea* sp. (who attacks host spiders) and *Ariamnes* spp. (who attack spiders that walk on their web lines) employ sticky-silk wrap-attack (*Rhomphaea* sp.: Whitehouse, 1987; *Ariamnes attenuatus*: O. P.-Cambridge, 1881; Eberhard, 1979).

Juvenile kleptoparasites activity is little registered on the literature. Cangialosi (1990) observed that *Faiditus ululans* (O. P.-Cambridge, 1880) juveniles tend to forage by searching undetected preys and, more rarely, sharing preys with the host spider. Whitehouse (1986), despite not describing juvenile *A. antipodianus* foraging with details, noted that the shared feeding with the host spider *Achaearanea* sp. is similar to the sharing of food between a mother theridiid spider and her offspring. This comparison led the researcher to propose that kleptoparasitism in Therididae may be an example of neoteny. Nevertheless, our observation on kleptoparasite spiderlings killing and eating the host spider *L. curacaviensis* do not conform to a mother-offspring relationship, but seems instead an ability to predate, opportunistically, the host spider.

Robbery versus theft

The occurrence of the behavior of shaking the web during the theft bout contrasts with our ingenuous expectative that kleptoparasites must act surreptitiously all the time and never be perceived by the host spider. Just as surprisingly as these behaviors, host spiders may run away because of these vibrations and leave the prey alone. These events show us another manner by which *A. elevatus* obtains food in host webs: the *robbery* of preys. We can distinguish prey *robbery* from prey *theft* because the first action is accomplished with aggressiveness and threatening behaviors.

Similarly, *F. ululans* can rob captured preys from the host *Anelosimus eximius* (Keyserling, 1884) (Theridiidae). The kleptoparasite approaches the prey while it is immobilized communally by many host spiders; just after the prey was subdued, the kleptoparasite vibrates the extended forelegs and shakes the web while walking towards the host spiders, chasing them away and taking the prey to the edge of the web (Cangialosi, 1990; 1991).

Argyrodes elevatus *is a true kleptoparasite*

Since Argyrodinae spiders commonly invade webs of spiders which are larger than themselves, particularly webs of giant *Nephila* spiders (Exline & Levi, 1962; Agnarsson, 2003), one may possibly think that the kleptoparasites do not cause any damage to the host, only utilizing ignored prey and taking very little while partaking of large preys. Henaut et al. (2005) suggest that if the diet of an invader organism does not overlap with the host spider diet, this invader must be called a kleptobiont. Moreover, they say that if it is possible to choose between many hosts, *Faiditus globosus* (Keyserling, 1884) tends to invade webs where it acts as a kleptobiont, and not as a kleptoparasite. Accordingly to these authors, this kind of preference could explain the high level of association between Argyrodinae and Nephila spiders around the world. Actually, an interaction can not be qualified as kleptoparasitism when there are no energetic costs (via loss of food) to the host (Iyengar, 2008).

However, Grostal and Walter (1997) demonstrated that the presence of the kleptoparasite *A. antipodianus* in webs of *Nephila plumipes* (Latreille, 1804) significantly reduces the gain of body mass by the spider. Rypstra (1981) showed an opposite relationship between kleptoparasite activity and prey capture rates in *N. clavipes* webs; it forces the host to change the web site more frequently. These accounts indicate true kleptoparasitim, even if the host body size was much larger than the kleptoparasite body size. Coyle et al. (1991) affirm that a single interruption in the feeding and the reaction with sharp movements, in response to an approaching kleptoparasite, are enough to qualify the interaction as a kind of parasitism, and not as a commensalism – since commensalism is an interaction in which there is no damage for the involved organisms (Abrams, 1987).

Despite our data not allowing a quantitative analysis, they endorse the idea that *A. elevatus* is not an irrelevant visitor as a commensalist or kleptobiont organism. We could see some strategies in the *A. elevatus* repertoire that are very deleterious to the host spider. Some of these behaviors are already known in the genus *Argyrodes* – as stealing captured prey (Vollrath, 1979), feeding with host (Robinson & Robinson, 1973), catching host spiderlings (Whitehouse, 1986) – and other behaviors are described only for other Argyrodinae genera – like the *robbery* (takeover with threat or violence) of preys performed by *Faiditus ululans* (Cangialosi, 1990; 1991). Moreover, we registered A. elevatus activities that are not described yet: theft of egg sacs and predation of host spider by kleptoparasite spiderlings. It is also a novel issue the fact that *A. elevatus* steals preys from *L. curacaviensis*, whose webs usually are not occupied by kleptoparasites in nature.

Finally, we could register that *A. elevatus*, just as the *Neospintharus trigonum* (Larcher & Wise, 1985; Cangialosi, 1997), can use wrap-attack to capture live preys in the host web. The wrapping employed by *A. elevatus* attacks is similar to the typical theridiid silk-sticky wrapping (Japyassú & Jotta, 2005; Garcia & Japyassú, 2005): it stands above the prey, reels the thread line to which the prey is attached and, with the fourth pair of legs, lays sticky silk on the prey. However, *A. elevatus* deposits a very little quantity of sticky silk on the prey if compared with non--kleptoparasite theridiid spiders, even juveniles. The wrapping speed is also very low; and, maybe because their legs IV are tiny, *A. elevatus* is aimless on wrapping prey: most of the sticky silk laid misses the prey. This apparently poor ability to catch its own preys and the wide range of foraging strategies employed demonstrate that *A. elevatus* is very well adapted to kleptoparasitic habits.

How to explain the high behavioral variability in Argyrodes elevatus*?*

Our data also provide an assembling of events that testifies the high behavioral variability of kleptoparasitic strategies. The data compiled in literature about others kleptoparasite species show that high levels of behavioral plasticity are not exclusive to *A. elevatus*, but are a common character in Argyrodinae spiders (Whitehouse et al., 2002; Agnarsson, 2004; Gonzaga, 2007). This plasticity is yet more impressive if we consider that theridiids have a predatory sequence stereotyped if compared with other web spiders (Japyassú & Caires, 2008). It leads to think that the subfamily Argyrodinae had an evolutionary change that increases significantly the foraging plasticity.

Finding that *A. elevatus* performs behavioral units that are not strictly linked to foraging during theft bouts, as agonism or web construction behavior (Silveira & Japyassú, unpublished data), we suggest that high plasticity in kleptoparasite and araneophagus Argyrodinae spiders is consequence of the simultaneity of different behavioral sets in action, while non-kleptoparasite spiders present these different behavioral sets in distinct moments. It is easy to think: a hypothetical kleptoparasite spider which walks on a host web towards a prey just captured presents, initially, behavioral units linked to foraging – just like a non-kleptoparasite theridiid spider. This walking, however, is unique: it is accomplished simultaneously with investigative behaviors as "rotary probe", because the host web is an unknown environment to the invader. Moreover, the host spider often may detect the kleptoparasite and attack it; it needs to be ready to carry out evasive or aggressive behaviors in response to this attack. Thus, in a single bout, a kleptoparasite is able to act simultaneously in different circumstances, such as foraging, exploring of new sites or agonist context, while a non-kleptoparasite theridiid spider presents each behavioral condition at different times.

Since the main difference between kleptoparasite and non-kleptoparasite spiders is the kleptoparasite's capacity to have different behaviors simultaneously in different contexts, this capacity may be the key to understand the evolution of kleptoparasitism in Argyrodinae.

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