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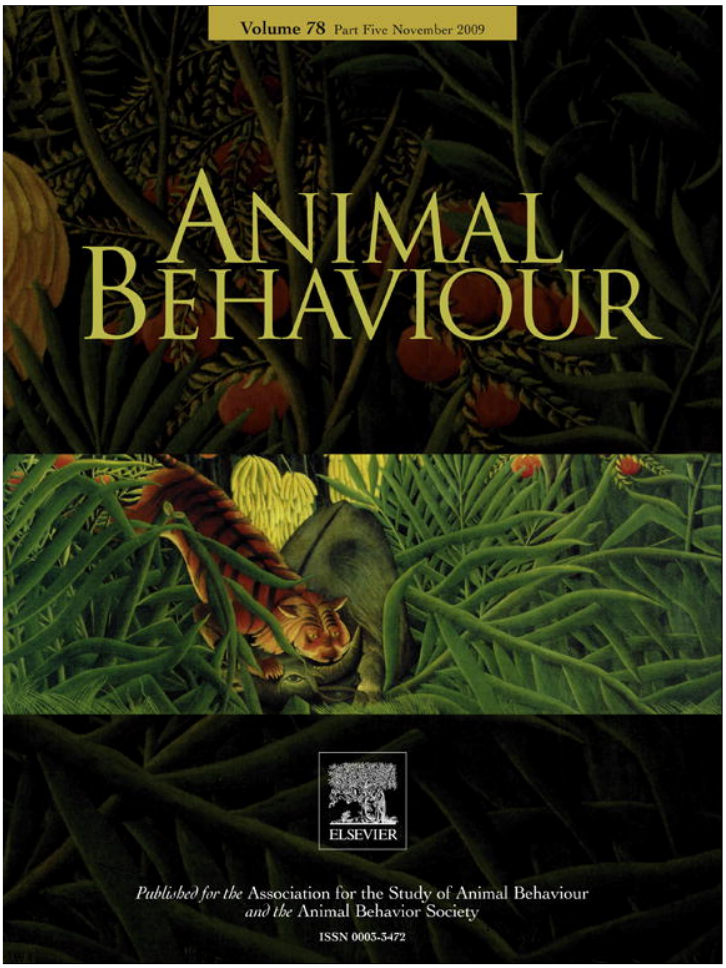

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Sex-specific kleptoparasitic foraging in ant-eating spiders

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Foraging by intraspecific kleptoparasitism is widespread among animal taxa. Most kleptoparasitic interactions are considered facultative, and can be influenced by life history stage and trade-offs with other activities such as mate searching. Trade-offs with mating strategies are often sex specific when males are selected to invest in mate searching while females engage in foraging to maximize fecundity. As a result, sexual dimorphism in opportunistic foraging may evolve, and would predict an ontogenetic shift from the juvenile to the adult stage where males could adopt opportunistic foraging. To investigate this hypothesis, we studied the effect of sex and life history stage on the frequency of kleptoparasitism in ant-eating spiders of the genus *Zodarion* in the field. These spiders use a special capture technique involving a quick attack on an ant that is left unguarded by spiders for several minutes, providing ample opportunities for kleptoparasitism. We found that adult females consistently hunted actively, while adult males ceased active prey capture and instead engaged in kleptoparasitism. Juvenile spiders were active hunters irrespective of sex. Consistent with an ontogenetic shift in foraging behaviour from hunting to kleptoparasitism in males, males preferred to feed on dead (freshly killed) prey while females preferred live prey. Furthermore, males experienced a decline in prey capture rate compared with females and juveniles. Kleptoparasitism in males was accompanied by inspection of female foraging sites, suggesting that males cease active prey capture and maximize mating opportunities.
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Kleptoparasitism, the exploitation of resources gathered by other individuals (Brockmann & Barnard 1979), is a widespread foraging strategy found across a range of animal taxa (e.g. snails: Pernet & Kohn 1998; Iyengar 2002; spiders: Christenson 1984; reptiles: Hayes 1987; birds: Brockmann & Barnard 1979; humans: Winterhalder 1996). In most cases kleptoparasitism appears to be facultative, suggesting that this trait is shaped by trade-offs between the opportunity and benefit of stealing a meal and the cost of engaging in kleptoparasitic interactions with the host (Iyengar 2008). These costs and benefits in turn vary with the life history stage and reproductive status of individuals.

In addition, kleptoparasitism allows the shift of investment of time and energy from foraging to other activities such as searching for mates or avoidance of predators (Iyengar 2008). Such activities often differ between the sexes, as males are commonly selected to invest more energy in search of mates or in male–male competition, while females must instead allocate resources to egg production and offspring care (Trivers 1972; Andersson 1994; Hunt et al. 2004). Hence, females may be required to invest more in foraging, while males should rather invest in mate searching. These intersexual differences can then be expected to result in sex-specific foraging strategies (Arnqvist et al. 2006). Indeed, kleptoparasitism by roaming males that share or steal food collected by females has been reported (Riedman & Estes 1988; Funston et al. 1998; Schneider & Lubin 1998; West & Toft 1999; Erez et al. 2005). The evolution of sex-specific dimorphism associated with trophic structures, such as smaller venom glands in males (e.g. Walker & Rypstra 2002), and rooted in differential reproductive strategies might result in an ontogenetic shift in foraging strategy (Badyaev 2002), where only adult males are expected to adopt an opportunistic foraging strategy. Here we examined this hypothesis in spiders.

Spiders of the genus *Zodarion* are specialized active hunters of ants (Pekár 2004a). Adult males and females and all juvenile developmental stages aggregate around ant nests and ant trails during concentrated bouts of hunting, which provide ample opportunities for intraspecific interactions. The spiders use a specialized capture technique involving a quick attack on an ant that is subsequently left unguarded for several minutes on the trail until the venom takes effect (Pekár 2004b). An attacked ant is likely to release alarm pheromones and attract other foraging ants. By leaving the bitten ant unguarded, the spider avoids the risk of injury from bites by other ants. Only when the ant is immobilized

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does the spider return to retrieve the prey, which it consumes at a safe distance from the ant trail where ants are very aggressive. Until the ant has been immobilized, the spider is at particular risk of losing its prey to a conspecific kleptoparasite.

We examined the effect of sex and life history stage on the frequency of kleptoparasitism in the field, to obtain quantitative data on sex-specific foraging strategies, and to test the hypothesis that males undergo an ontogenetic shift from active prey capture to kleptoparasitic behaviour, consistent with expectations of sexual divergence in foraging investment.

METHODS

We performed field observations from June to September in southern Portugal in a semidesert habitat near Mértola. Here, polymorphic ants of *Messor barbarus* (Linnaeus), where worker morphs vary in body length from 3 to 11.5 mm, are hunted by *Zodarion jozefienae* (Bosmans) spiders (total body length: 3–3.4 mm in males, 3.0–5.7 mm in females). We identified the spiders using Bosmans (1994) and Pekár et al. (2003) and ants using Collingwood & Prince (1998). As both the ants and the spiders are nocturnal, we made observations between 2000 and 0400 hours. We marked ant nests with a flag and removed grass from the ant trails (about 5 m long) a day in advance to facilitate observations.

We performed observations at 40 ant nests during approximately 200 census-hours. A single observation consisted of following a spider for at least 5 min (up to 30 min). Its behaviour was classified into one of four categories: 'patrolling' if the spider was walking up and down the trail without attacking ants; 'hunting' if the spider captured an ant; 'sharing' if the spider did not participate in hunting but was consuming the same ant with another spider; and 'stealing' if the spider took an ant paralysed by a different individual and consumed it alone. 'Patrolling' males were presumably searching for mates. Afterwards we collected and identified individual spiders to developmental stage and sex.

For laboratory experiments we collected *Z. jozefienae* spiders a week before the experiments. We fed the spiders with a single *M. barbarus* ant and then left them without food for 5 days at approximately 25 °C. In a choice experiment, one live and one dead *M. barbarus* ant of a similar size (medium–large morph, 8–10 mm body length) were placed at opposite sides in a petri dish with a polystyrene bottom (diameter 50 mm). The live ant was fixed to the bottom of the dish with a short string to standardize the number of encounters. An ant that had been frozen (−25 °C) for 15 min and then left for another 5 min at ambient temperature was presented as freshly killed prey. We tested the preference of males, females and juveniles for live versus freshly killed prey by releasing a spider on the centre of the dish, and recording which ant it attacked and fed on. Each trial was ended after the first item was consumed. Juvenile spiders were then reared until the adult stage and sexed.

In a second experiment, we compared the relative proportion of successful prey capture events between male, female and juvenile spiders. We used a similar standardization of hunger level as in the previous experiment. A spider was placed in a petri dish (diameter 35 mm) and offered one small–medium *M. barbarus* ant (5–7 mm body length) and capture success (binomial) was recorded in trials that lasted until the ant was captured, or for a maximum of 60 min.

In the field, ants that have been captured by spiders and from which body fluids have been extracted are discarded seemingly intact close to the ant trails (these spiders are extra oral digesters that extract fluids from the prey without destroying the cuticle). Such discarded empty corpses may not easily be distinguished by kleptoparasites from freshly immobilized prey (Pekár 2004b); hence we investigated the preference for feeding on discarded versus freshly killed ants in a third choice experiment. We used only males and juveniles because these were found to kleptoparasite ants in the field. Male ($N = 25$) and juvenile ($N = 30$) *Z. jozefienae* spiders were placed in a petri dish (diameter 35 mm) and were offered two *M. barbarus* ant corpses: one freshly killed obtained by freezing an ant (at −25 °C) for 15 min and one 24 h-old discarded ant obtained from a female *Z. jozefienae* that had fed on it the previous day. The feeding preference and consumption time were recorded.

We analysed data using statistical methods in R (R Development Core Team 2007), specifically by generalized linear models (GLM) with an appropriate error distribution and a link function. For counts we used the Poisson family (GLM-p), and for proportions the binomial family (GLM-b), both with their canonical link functions (Crawley 2002). Adequacy of the models was examined from diagnostic plots. Post hoc differences between expected values were compared by means of treatment contrasts. We used the exact binomial test to compare observed and expected frequencies, the two-sample test for equality of proportions to compare two proportions and the Welch test to compare consumption durations with unequal variances.

RESULTS

In the field, male, female and juvenile spiders showed significantly different foraging behaviour. The interaction between behaviour and class of individuals was significant (GLM-p: $\chi^2_4 = 398$, $P < 0.0001$; Fig. 1). Most females (88%, $N = 132$) and juveniles (81%, $N = 129$) actively hunted ants, whereas only 2.4% of the males ($N = 212$) performed active hunting (treatment contrast: $P < 0.0001$). The remaining individuals patrolled the ant trail. Excluding patrolling individuals, no females attempted kleptoparasitism, while 81.5% of males ($N = 27$) and 7% of juveniles ($N = 112$) were observed to steal prey. In all cases the kleptoparasitized prey was a freshly attacked ant (see video in Supplementary Material). In 62% ($N = 29$) the stolen ant was taken from adult females and in 38% from juveniles. Only females (27%, $N = 132$) attacked more than one ant during the observation periods. No spiders ($N = 225$) shared prey.

The choice experiment showed that all spiders sampled the prey by tapping both the dead and the live tethered ant. However, males, females and juveniles displayed significantly different preferences (GLM-b: $\chi^2_2 = 21.4$, $P < 0.0001$; Fig. 2): the majority of females (92%,

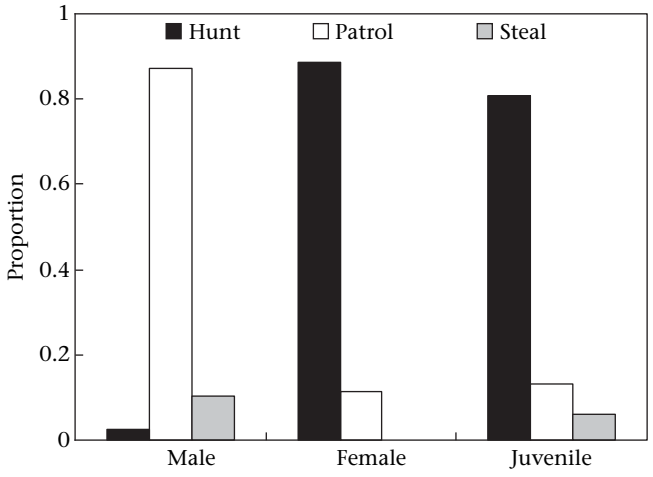

Figure 1. Frequencies of active hunting, patrolling of foraging sites and kleptoparasitic interactions of male, female and juvenile *Z. jozefienae* spiders in the field.

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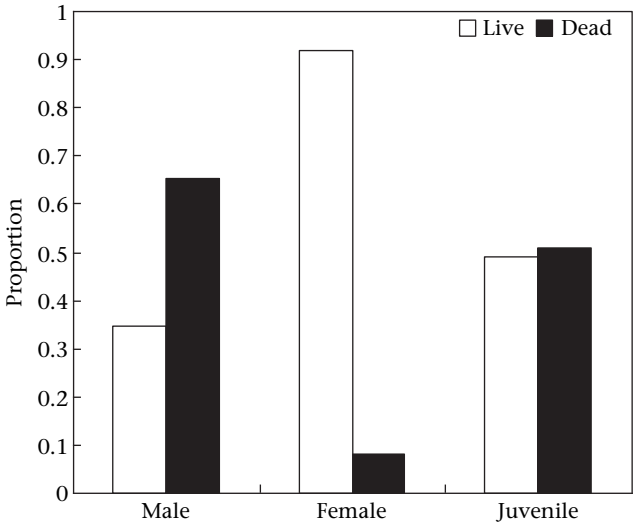

Figure 2. The proportion of male, female and juvenile *Zodarion* spiders choosing a live or a dead ant in a choice experiment.

$N = 25$) chose the live ant, while 51% ($N = 63$) of juveniles and 65% ($N = 23$) of males chose the dead ant. The preference of juveniles thus differed significantly from that of females (contrast: $P = 0.0008$) but not from that of males (contrast: $P = 0.35$). There was no difference in preference between sexes in juveniles (two-sample test for equality of proportions: $\chi^2_1 = 0.13$, $P = 0.72$): 47% ($N = 47$) of juvenile females and 56% ($N = 16$) of juvenile males chose to feed on a live ant.

The proportion of prey capture events differed significantly between males, females and juveniles (GLM-b: $\chi^2_2 = 20$, $P < 0.0001$). Males had a significantly lower capture rate (70%, $N = 40$) than females (100%, $N = 40$) and juveniles (93%, $N = 40$; treatment contrasts: $P < 0.0001$). The frequency of kleptoparasitism of males, females and juveniles observed in the field (Fig. 1) thus strongly correlated with their capture success in experimental trials (Pearson correlation: $r_1 = -0.92$, $P = 0.26$).

In the choice between freshly killed and discarded ants, males and juvenile spiders showed a similar high preference for fresh corpses (exact binomial test: $P < 0.0001$; Fig. 3; pooled mean for both classes = 0.93, 95% confidence interval = 0.84, 0.98). While spiders consumed a fresh corpse for at least 2 h, an old corpse was consumed on average for 8 min with a maximum of 1 h (Welch test: $t_{19.4} = 25.6$, $P < 0.0001$).

Figure 3. Comparison of proportion of male and juvenile *Zodarion* spiders that fed on a freshly killed compared with a 24 h-old ant that had been previously fed on.

DISCUSSION

Our results showed distinct sex-specific foraging patterns: in the field, adult females exclusively relied on active prey capture, while adult males foraged by kleptoparasitism. More than 80% of the males were not observed to forage at all, suggesting that males to a large extent cease active hunting and, for foraging, rely entirely on kleptoparasitic interactions. This conclusion based on field data was supported by laboratory experiments on prey capture rate showing that the shift to kleptoparasitism in adult males correlated with a significant decline in capture rate. Accordingly, males preferred to feed on dead (freshly killed) ants while females foraged exclusively on live ants, further demonstrating sexual dimorphism in feeding preference. The field study showed that juvenile spiders predominantly foraged by active prey capture independent of sex, implying that males adopt opportunistic foraging upon sexual maturation. The sex ratio (males:females) of the wild population of *Z. jozefienae* ($N = 324$) was 1.5:1 (S. Pekár, unpublished data). Our study thus provides quantitative evidence for two findings: first, we have shown that sex-specific foraging strategies arise through an ontogenetic shift from active prey capture in juveniles to kleptoparasitism in males. Quantitative data on sex-specific kleptoparasitism appear to be surprisingly scarce as most papers have reported only anecdotal observations on male kleptoparasistism, and have not provided an estimate of its frequency in a population (e.g. Vollrath 1980). Second, not only did males become kleptoparasites, they remarkably almost completely ceased active prey capture and adopted an obligatory kleptoparasitic foraging strategy despite patrolling patches with abundant prey.

Intraspecific kleptoparasitism is common in social or colonial animals (e.g. Brockmann & Barnard 1979), and has been modelled as 'producers' (provide prey) and 'scroungers' (steal prey; Barnard 1984). In species where food sharing is common, scroungers should have a negligible effect on producers' gain (e.g. Barnard & Sibly 1981), and the chance of capturing prey should be spread equally among individuals as a reciprocal 'Tit for Tat' strategy because the now-scroungers can be next-time-producers (Giraldeau et al. 1994). Food sharing has been observed in captive juvenile *Zodarion cyrenaicum* Denis (Pekár et al. 2005). However, our results do not fit such scrounger–producer games because the exclusive kleptoparasitic strategy was mainly seen among adult males. These have lower capture success than adult females and juveniles. The asymmetry in kleptoparasitic behaviour is consistent with data on oystercatchers, *Haematopus ostralegus*, and kelp gulls, *Larus dominicanus*, that feed on mussels, *Mytilus edulis* (Goss-Custard & Durell 1987; Steele & Hockey 1995). In these systems younger juveniles that were inefficient hunters relied more heavily on kleptoparasitism of mussels from adults than older juveniles and adults.

Although males and females of *Zodarion* spiders can hunt in close proximity to each other, the hunting (searching, attack and consumption) takes a long time; thus the males are expected to trade off energy and time investment between hunting and mate searching. The intake rate of males is about 2.5 times lower than that in females and correponds to the sexual dimorphism in body size as well as in trophic structures (chelicerae and venom glands; S. Pekár, unpublished data). Yet to obtain even a small prey mass males spend more than 2 h feeding on their prey. Female *Zodarion* spiders are polyandrous and were observed to mate with several different males at the foraging sites during a single hunting event (S. Pekár & M. Martišová, unpublished data). We have observed few male–male interactions in the vicinity of females suggesting that

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increased body size may provide males with an advantage in intrasexual competition. The ontogenetic shift in foraging strategy observed in *Zodarion* males thus suggests that adult males invest time and energy in mate searching combined with kleptoparasitism of the female's prey. The capture of ants is associated with the risk of being injured, as worker ants are notoriously aggressive (Pekár 2004b), in addition to the energy expenditure of prey capture per se. Hence, it is likely that kleptoparasitism as a foraging strategy is less costly than active hunting. Furthermore, kleptoparasitism that involves locating of females' prey will provide males with access to mates. Our finding that males preferred freshly killed prey to discarded corpses indicates that males are indeed obtaining a valuable meal through kleptoparasitism. In addition, low-cost opportunistic foraging in males may facilitate mate-searching activities.

During inactivity *Zodarion* spiders hide in tightly sealed, small, igloo-shaped retreats that probably provide safe shelter from nearby ants (Pekár & Král 2001). We have observed plenty of matings ($N = 54$) but only at and near to ant foraging trails. *Zodarion* females are thus only accessible to males when they forage and, hence, male patrolling of female foraging sites is consistent with a male strategy to secure mates and maximize reproductive success. While males are also successful in securing a meal by kleptoparasitism, the relatively low rate of prey stealing relative to patrolling effort indicates a shift in energy investment in males from foraging to securing reproductive opportunities (Andersson 1994; Hunt et al. 2004; Kokko & Jennions 2008).

A similar shift in kleptoparasitic behaviour has so far been reported for few web-building spider species. Males of some web-building spiders lose their ability to build capture webs and move on to the female's web. If such cohabitation lasts for a few days, males may capture prey at the female's web and thus compete with her for prey (Suter 1985), or feed on items that the female has captured (Vollrath 1980). In *Nephila*, where multiple males live on a single female web, the ones that are on the edge of the web compete for neglected prey with interspecific kleptoparasites or consume the silk (Vollrath 1980). In these cases, males' kleptoparasitism is expected to be negligible to the females' fitness, but stealing the entire ant by *Zodarion* males is likely to cause considerable cost to females and juveniles. The costs, however, remain to be estimated.

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Supplementary Material

Supplementary information associated with this article can be found, in the online version, at doi: doi:10.1016/j.anbehav.2009.07.025.

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