

Fleur E. Champion de Crespigny
Marie E. Herberstein · Mark A. Elgar

Food caching in orb-web spiders (Araneae: Araneoidea)

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Abstract Caching or storing surplus prey may reduce the risk of starvation during periods of food deprivation. While this behaviour occurs in a variety of birds and mammals, it is infrequent among invertebrates. However, golden orb-web spiders, *Nephila edulis*, incorporate a prey cache in their relatively permanent web, which they feed on during periods of food shortage. Heavier spiders significantly reduced weight loss if they were able to access a cache, but lost weight if the cache was removed. The presence or absence of stored prey had no effect on the weight loss of lighter spiders. Furthermore, *N. edulis* always attacked new prey, irrespective of the number of unprocessed prey in the web. In contrast, females of *Argiope keyserlingi*, who build a new web every day and do not cache prey, attacked fewer new prey items if some had already been caught. Thus, a necessary pre-adaptation to the evolution of prey caching in orb-web spiders may be a durable or permanent web, such as that constructed by *Nephila*.

Introduction

Many animals store food for later ingestion, rather than consuming it immediately after acquisition. Caching food allows animals to capitalise on short-term fluctuations in food abundance by capturing surplus prey items and storing them for consumption during leaner periods (Lea and Tarpay 1986; Vander Wall 1990; Hurly 1992). This behaviour may reduce the risk of starvation in an environment of unpredictable or variable food supply (McNamara et al. 1990). The decision to store food externally, rather than internally as fat, depends on the en-

ergetic value of a cacheable food item (Kotler et al. 1998) together with the relative costs and benefits of external and internal storage. Ingesting food immediately secures the nutrients, but there may be physiological limits to the amount of food that can be stored as fat, or the amount of food an individual can ingest during a foraging bout (Johnson et al. 1975). Furthermore, the high cost of maintaining large fat reserves may outweigh their energetic benefits (Cuthill and Houston 1997). Some of these problems are overcome if the food is stored externally, although costs associated with caching food include travel costs, mistakes in cache relocation and the danger of the food stores being pilfered by rivals (McNamara et al. 1990).

Food hoarding is typically associated with birds and mammals (Sherry 1985; Lea and Tarpay 1986; Vander Wall 1990; Hurly 1992; Kotler et al. 1998). Food storage is less common in invertebrates, and is primarily connected with provisioning offspring. For example, many species of insects construct nests that contain food for the developing larvae (review in Choe and Crespi 1997), while ants and certain bees cache food both for individual consumption and for brood provisioning (see Vander Wall 1990). Hoarding for individual consumption is not common in invertebrates, but has been reported in the crab, *Pilumnus vespertilio* (Kyomo 1999), which carry algae into their burrows. Food caching is more widespread in spiders (Eberhard 1967) that wrap prey for later ingestion. However, the length of time that the food is stored in this way is usually relatively short (hours to days) compared with the weeks and months that is typical of mammals and birds (Vander Wall 1990).

Some species of orb-web spiders (Araneoidea) leave prey remains attached to the web for several weeks. For example, species of *Nephila* incorporate a densely packed, conspicuous, vertical band of uneaten prey and prey remains in their webs. These so-called rubbish bands (*sensu* Main 1976) are usually located directly above the central hub of the web. The function of these 'rubbish bands' has not been investigated experimentally

F.E. Champion de Crespigny · M.E. Herberstein · M.A. Elgar (✉)
Department of Zoology, University of Melbourne, Victoria 3010,
Australia
e-mail: m.elgar@zoology.unimelb.edu.au
Tel.: +61-3-83444338, Fax: +61-3-83447909

Present address:

M.E. Herberstein, Department of Biological Sciences,
Macquarie University, NSW 2109, Australia

(Herberstein et al. 2000), but they may deflect predatory attacks away from the spider (Edmunds and Edmunds 1983) and/or they may be more accurately described as food caches. Orb-web spiders that cache food may benefit from obtaining a relatively constant prey ingestion rate even if the rate at which prey encounter the web is temporally variable. However, this benefit can only apply to those species that build relatively permanent webs and repair only the damaged sections, because spiders that rebuild the entire web every day or move web locations frequently will be unable to stockpile prey in the web.

Two similar sized, Australian orb-web spiders, *Nephila edulis* and *Argiope keyserlingi*, build orb-webs that are typical of their genus. The web of *N. edulis* is a relatively permanent structure, and the female only repairs damaged sections rather than dismantling the entire web (see Robinson and Robinson 1976; Vollrath 1985; Elgar 1989). The webs of both adult and sub-adult spiders may contain rubbish bands. In contrast, webs of *A. keyserlingi* do not contain rubbish bands and the female dismantles her web and spins a new one daily and sometimes even more frequently (see Craig 1989). Any prey remaining in these webs may be lost during this process. We investigated experimentally whether spiders of *N. edulis* feed on the prey remains to minimise weight loss during periods of food deprivation. We also compared the attack behaviour of both species during periods of multiple prey encounter. Specifically, we predicted that *N. edulis* will always attempt to capture prey, irrespective of the number already captured. This behaviour was not expected in *A. keyserlingi*, because it will eventually expend energy capturing prey it is unlikely to consume.

Materials and methods

Immature female spiders of *A. keyserlingi* and *N. edulis* were collected in Sydney, New South Wales and Euroa, northern Victoria, respectively. The spiders were maintained in the laboratory in up-turned plastic cups and were fed an *ad libitum* diet of bush-flies (*Lucilia cuprina*) until they reached maturity. Once mature, the spiders were transferred to three-dimensional, perspex frames (58×58×15 cm) where they constructed typical orb-webs. All the spiders used in the experiments had mated, and were maintained on a constant diet of bush-flies before the experimental treatments. All webs were lightly sprayed with water at least every alternate day.

Food caches, food deprivation and weight loss

Fifty adult female *N. edulis* were randomly allocated to one of two experimental treatments that altered the presence of rubbish bands. In the experimental treatment, the prey remains were excised out of the web of each spider. The prey remains were left intact in the control treatment, but an equivalent, adjacent, area of silk was excised. The frames that housed the spiders were swept clean of all prey remains and any other uneaten prey items were removed from webs. The spiders were not fed for 10 days, although their webs were sprayed with water twice weekly. The weight and the combined tibia–patella length of the first leg of the spider, and the length of the band of prey remains were measured at the start and

end of the 10-day food deprivation period. Data from spiders that laid egg sacs or died during this time were excluded from the analysis.

Food caches and attack behaviour

We examined the patterns of attack behaviour of the two species by subjecting spiders to one of three pre-experimental treatments, followed by the experimental trial. Thirty adult female spiders of *A. keyserlingi* and of *N. edulis* were randomly assigned to one of three pre-experimental treatments in which they were provided with either zero, five or ten bush-flies immediately prior to the experimental trial. Using forceps, we placed the bush-flies on the web, within a 5-cm radius of the hub. The spiders only attacked and wrapped each prey item, returning to the hub without ingesting any prey. The experimental trial commenced immediately after the spider had attacked and wrapped the final pre-experimental prey item. Using forceps, we placed a single bush-fly onto the lower half of the web, 20 cm from the hub. We noted whether the spider then attacked or ignored this offered prey. We recorded a rejection if the spider did not attack the prey within 2 min of its introduction. Prey items that did not struggle continuously were replaced, and the time restarted in order to ensure that appropriate vibration cues were transmitted to the spider.

Results

Of the 50 spiders that were used in the experiment, 21 laid egg sacs or died during the experiment and were consequently excluded from the analyses. The initial weight ($t_{27}=0.34$, $P=0.7$), tibia–patella length ($t_{27}=0.13$, $P=0.9$) and cache size ($t_{27}=0.38$, $P=0.7$) of spiders did not differ between the two treatments. The length of the food cache was positively correlated with the initial weight of the spider ($r_{28}=0.374$, $P<0.05$; Fig. 1).

Analysis of variance of the variation in weight loss revealed a significant interaction between initial weight, cache size and experimental treatment ($F_{1,22}=6.11$, $P<0.05$). Thus, we correlated weight loss with the initial weight of the spiders within each treatment. When the food cache was removed, heavier spiders lost significantly more weight than lighter spiders ($r_{14}=0.597$, $P<0.02$; Fig. 1). However, this relationship disappeared when spiders were able to access caches throughout the deprivation period ($r_{13}=0.243$, $P>0.3$).

The experimental introduction of prey onto the webs of *N. edulis* and *A. keyserlingi* revealed two foraging strategies (Fig. 2). The *N. edulis* spiders attacked most of the prey they encountered, irrespective of the number of prey they had previously captured ($\chi^2_2=0.38$, $P>0.13$). In contrast, *A. keyserlingi* always attacked the experimental prey if they had not previously captured any bush-flies, but they were more likely to ignore new prey if they had already captured five or more prey items ($\chi^2_2=6.67$, $P<0.04$). The spiders were apparently aware of the new prey items because they often tugged the radial strands of the web leading to the prey item.

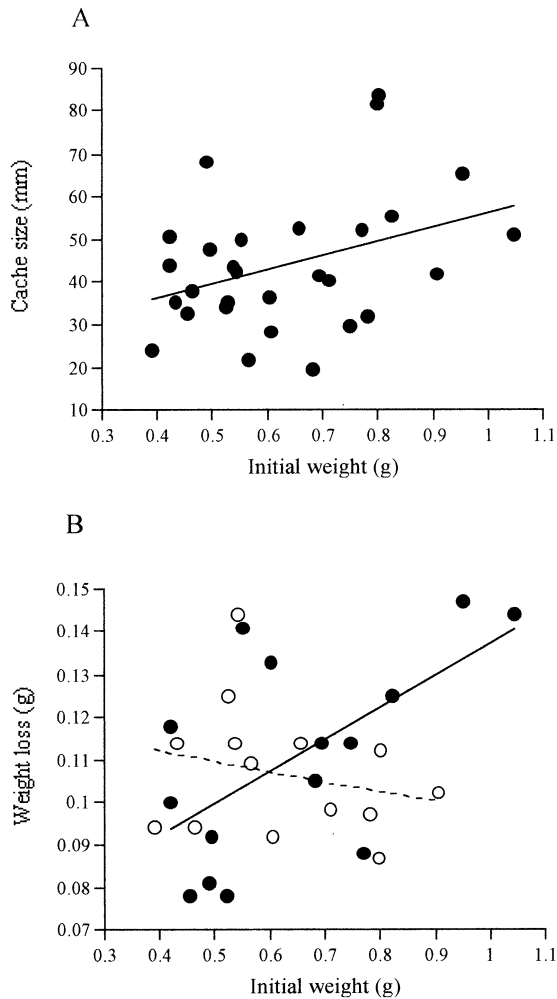


Fig. 1 The relationship between the initial weight of females of *Nephila edulis* and **A** the size of the food cache in their webs (length, mm), and **B** the amount of weight lost (g) for spiders that retained their food cache (○ broken line), and those that had their cache removed (● solid line)

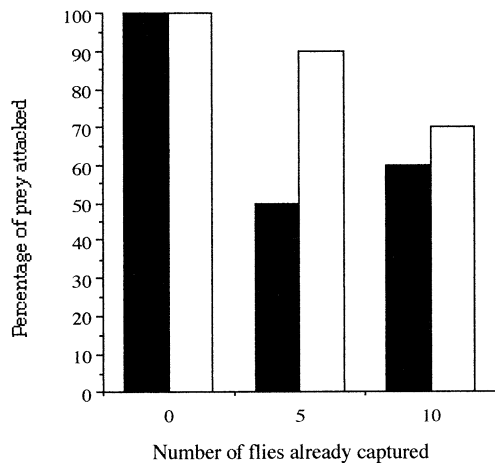


Fig. 2 The percentage of *Argiope keyserlingi* (black columns) and *Nephila edulis* (white columns) that attacked the experimental prey item after capturing either zero, five or ten flies during the pre-experimental treatment

Discussion

Our data reveal two lines of evidence that the ‘rubbish bands’ incorporated into the webs of *N. edulis* and other species of this genus (see Herberstein et al. 2000) are food caches. First, adult females of *N. edulis* reduce weight loss during periods of low rates of prey encounter by supplementing their diet with previously captured prey. The experiments indicated that these food caches may be especially important for heavier spiders, which lost 1.5 times more weight in the absence of a cache. In contrast, spiders with a food cache experienced a similar weight loss irrespective of their initial weight. The reason for this difference may be that lighter spiders tended not to utilise caches and also tended not to build them. Furthermore, the variation in the weights of our sample of spiders reflects differences in the amount of fat and/or eggs stored in the abdomen, rather than differences in their overall body size. Thus, heavier spiders may sustain greater metabolic costs than lighter spiders because the former will be maintaining a larger number of eggs internally. Additionally, heavier spiders may have more fat reserves to lose than lighter spiders; perhaps the lighter spiders would have perished if the experimental period of food deprivation had been longer. Nevertheless, the presence of a cache appears to benefit heavier spiders more than lighter spiders. Consistent with this interpretation is the observation that heavier spiders cache more prey than lighter spiders do.

The second line of evidence concerns the attack behaviour of the different spiders, which was consistent with a food caching explanation for the rubbish bands. The *N. edulis* spiders continued to attack prey as it entered the web, since the prey could be stored for subsequent consumption. In contrast, *A. keyserlingi* spiders ceased to attack prey after several previous successful captures. Orb-web spiders do not capture prey indiscriminately, but often reject prey that is unsuitable or does not suit their metabolic requirements (Herberstein et al. 1998). Furthermore, capturing prey can be costly for spiders: energy is expended during the attack, spiders may be exposed to predators or unfavourable conditions and they may incur injury from the struggling prey (Riechert and Maupin 1998). In that context, it is surprising that ‘surplus killing’ (*sensu* Kruuk 1972) in the absence of food caching is sometimes observed in spiders (Samu and Bíró 1993; Riechert and Maupin 1997).

Spiders are generally thought to be food limited (Wise 1993), but few have evolved a food caching strategy. Low prey intake, variable food supply and the costs associated with fat storage favour the evolution of food hoarding (McNamara et al. 1990). However, web site tenacity and durability may also be necessary pre-conditions for food caching. The webs of adult *Nephila* usually remain at the same location for several weeks and only the damaged sections of the webs are repaired (Robinson and Robinson 1976; Vollrath 1981; Elgar 1989). Changing web location in response to food stress may be costly for *Nephila* because their webs are ener-

getically expensive (Vollrath 1981). Indeed, 'rubbish bands' are commonly found on webs of other spiders, such as *Cyrtophora*, which also build relatively permanent webs (see Herberstein et al. 2000). In contrast, the webs of *A. keyserlingi* are much less durable and must be entirely reconstructed at least once each day (Bristowe 1958; Craig 1989). These spiders are also more likely to move if they experience low prey capture rates (e.g. McNett and Rypstra 1997; Nakata and Ushimaru 1999; Chmiel et al. 2000), whereas *Nephila* are not likely to change web location in response to habitat quality (Vollrath and Houston 1986).

Prey caching has not been reported for other spider species that do not build orb-webs but nonetheless construct permanent and durable webs. Food storage may be more frequently observed among orb-web spiders because the construction of vertical adhesive orb-webs has been a 'key innovation', resulting in a comparatively greater radiation and species diversity compared with other families (Opell 1997, 1998; Bond and Opell 1998). Furthermore, vertical orb-webs intercept and retain prey more efficiently than sheet or tangle webs (Rypstra 1982). Therefore, spiders in vertical adhesive orb-webs may capture surplus prey that may be stored in permanent webs. Hence, high prey capture success, durable orb-webs and permanent web sites may have provided suitable conditions for the evolution of prey caching behaviour. This in turn has further influenced the attack behaviour of spiders.

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