

**Frequency, composition and variation in
external food stores constructed by orb-web spiders:
Nephila edulis and *Nephila plumipes* (Araneae : Araneoidea)**

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Abstract

Few examples of food hoarding have been documented in spiders, yet two Australian species of orb-web spiders, *Nephila edulis* and *N. plumipes*, typically incorporate previously captured prey into the web. The effect of prey density and prey-encounter rate on the storage behaviour of adult female *N. edulis* was tested in the laboratory. Prey density had a significant effect on the propensity to construct external caches: when more food was available, food caches were larger than when the supply of prey was limited. Caching behaviour also differed with the rate of prey encounter, even though the total amount of food supplied was the same. When prey were encountered at constant rates, spiders allocated more food to external storage compared with random encounter rates. Finally, we tested the quality of different prey types for external or internal storage. *N. edulis* were fed with blow-flies or crickets, and these prey were stored in the web, discarded or totally consumed. Crickets were typically consumed or stored, while flies were more frequently discarded. Field observations of the storage behaviour in *N. edulis* and *N. plumipes* found surprising differences in the composition of the cache. While *N. plumipes* incorporated only animal material, *N. edulis* also utilised plant material, suggesting that the storage band in *N. edulis* has other, non-food-storing functions. Field experiments indicated that the presence or absence of external stores in the web of *N. plumipes* had no influence on mortality, weight gain, or the presence of *Argyrodes* kleptoparasites.

Introduction

Foraging has two major components, the acquisition of food and the maintenance of these acquired resources. The former consists of searching, handling and ingestion of food, and these resources can be maintained internally as fat deposits or externally as short- or long-term caches (Stephens and Krebs 1986). Storing food resources internally by eating them immediately has the advantage that the nutrients are secured as fat. On the other hand, most animals are physiologically limited in how much they can eat at any one time and how much fat they can store (Johnson *et al.* 1975). Furthermore, a higher body mass due to fat storage requires an elevated metabolic rate and decreases mobility, thereby increasing the risk of predation and lowering foraging efficiency (e.g. Witter and Cuthill 1993).

Maintaining external food storages is an alternative to internal fat stores and occurs among many animals (see Vander Wall 1990). External caches may reduce the risk of starvation by reducing the variation in food intake during times of low food availability (McNamara *et al.* 1990). Nevertheless there are disadvantages associated with food hoarding. Animals may have problems relocating the cache, the cache may be pilfered (Leaver and Daly 2001), and/or the food may be spoilt by mould, germs or parasites. Furthermore, searching for external stores involves higher travel costs and may increase exposure to predators and unfavourable conditions (McNamara *et al.* 1990). Clearly, the future value of stored food depends on nutrient and energy content and the likelihood of consumption later on (Andersson and Krebs 1978; Moreno *et al.* 1981; Kagel *et al.* 1986).

Food hoarding is widely documented in birds and mammals and has evolved several times independently (Andersson and Krebs 1978; Smith and Reichman 1984; Sherry 1985; Stevens and Krebs 1986; Vander Wall 1990; Leaver and Daly 2001). Among invertebrates, the classic examples of food hoarding are found among social insects such as honeybees and ants (see Vander Wall 1990).

In spiders, two types of hoarding behaviour have been described. Short-term storage involves wrapping the freshly captured prey in silk and leaving it in the web for later consumption (Eberhard 1967). Generally, spiders will ingest the wrapped prey at the end of their foraging period, typically after about 12–24 hours. Champion de Crespigny *et al.* (2001) documented a long-term storage mechanism (several days to weeks) in the orb-web spider *N. edulis* (Tetragnathidae). This spider, like other congeners, incorporates a densely packed conspicuous band of previously captured uneaten prey and prey remains in their web (Main 1976). *N. edulis* can maintain body mass in periods of low prey capture by ingesting the stored items, a strategy that is particularly evident for larger individuals that also tend to store more prey at the hub (Champion de Crespigny *et al.* 2001).

Spiders are extra-oral fluid feeders that can ingest enormous amounts of food relative to body mass due to the presence of gut diverticula (Foelix 1992). Thus they may not be limited by the amount of food they can ingest. Nevertheless, weight gain through internal food storage is still costly as it interferes with locomotion (Herberstein and Heiling 1999). Despite physiological and behavioural adaptations to maximise food intake, spiders in general, and the genus *Nephila* specifically, experience limitations in food supply over time (Wise 1993).

A disadvantage of hoarding behaviour in web-building spiders is that the secured prey items may be lost to kleptoparasites or through web damage (Vander Wall 1990; Elgar 1993). Spiders in the genus *Nephila* are often host to kleptoparasitic spiders (Elgar 1993). For example, various species of *Argyrodes* (Theridiidae) collect tiny prey items from host webs (Exline and Levi 1962; Liao *et al.* 1984), share food directly with the host (Vollrath 1979) or steal prey from the host (Rypstra 1981). Additionally, they may ingest the web silk, incurring high costs for the host (Tso and Severinghaus 1998). Thus, storing food in the web may attract larger numbers of kleptoparasites as they may access caches more easily. An additional cost specific to spiders is that desiccated prey remains have to be re-liquefied to extract nutrients. Under dry or limited condition, spiders may not be able to access these external caches.

The present study examines prey-hoarding behaviour in two species of orb-web spiders, *N. edulis* and *N. plumipes*. These two species are widely distributed throughout the tropical and temperate regions of Australia. Both species incorporate a storage band into their web that is usually attached to the barrier web near the hub. We investigated the composition of the food caches constructed by *N. edulis* and *N. plumipes* and the food-storing behaviour with respect to prey availability. Specifically, we predicted that when prey density is high or prey-encounter rates are unpredictable, these spiders will store more prey externally than when prey is scarce or encountered at constant rates. Finally, field experiments were conducted to observe the relationship between food stores, weight gain, rates of mortality and the activity of kleptoparasites in the webs of food-storing females. We predicted that removal of the external stores would reduce weight gain in spiders and would reduce the density of kleptoparasites in the web. Finally, if these bands function to reduce predation by concealing the spider, we would expect spiders in webs without storage bands to suffer higher rates of mortality than spiders that retained the storage bands.

Material and Methods

Animal maintenance

Females of *N. edulis* were collected from Euroa (Victoria) and Brisbane (Queensland) and maintained in the laboratory at the University of Melbourne. All spiders were housed individually in upturned plastic cups (100 mm × 73 mm). They were fed *ad libitum* with Australian sheep blowflies, *Lucilia cuprina* (Diptera, Calliphoridae), and sprayed with water every second day. For experiments, females of variable ages (adult, penultimate, immature) were placed in three-dimensional Perspex frames (580 mm × 580 mm × 150 mm), where they constructed typical orb webs. During the experiments, the spiders were fed with blowflies (mean ± s.e. = 0.017 ± 0.0062 g, *n* = 2631) or crickets (mean ± s.e. = 0.152 ± 0.02 g, *n* = 38). Only those individuals that built regular webs and that did not die during the experiment were included in the analyses. In the field, the prey items are typically stored outside the web in the barrier web. Spiders do not build barrier webs in the laboratory because the frames are insufficiently deep, and so the food was stored in the orb web, above the hub and arranged as a vertical band.

Natural history of the storage band

N. edulis were observed under natural conditions at Euroa during February 2001 and *N. plumipes* during March 2001 in West Pymble Park (Sydney). The contents of the storage bands were investigated by excising the entire bands from a random subset of 25 adult female *N. edulis* and 49 adult female *N. plumipes* on the last day of observations. The stores were returned to the laboratory, dried in an oven at 180°C for 30 min and examined for animal and plant material using a dissecting microscope. Animal and plant components were weighed separately.

Field observations and continuous observations of storage-band growth do not allow for the band to be excised and weighed. Thus we have used band length as a reliable surrogate variable for weight as these two factors are significantly correlated ($r = 0.797$, $n = 123$, $P < 0.001$; data taken from laboratory webs). This provides better comparative data by using one common size variable for all experiments and field observations.

Prey density and food hoarding in N. edulis

This experiment examined variation in storage behaviour by providing prey at different densities using a paired design. Spiders that receive prey at high densities are predicted to store more prey than spiders that receive prey at low densities. Individuals were randomly assigned to two experimental treatments, and weighed before they were introduced into the frames. Spiders in the 'low-prey' treatment received one fly per day, while spiders in the 'high-prey' treatment received three flies per day. After seven days, the storage band was measured (length) with callipers and the spiders were weighed on the same day, and returned to their frames for another seven days, during which spiders in the 'low-prey' treatment were fed excess flies to even out both treatments. The spiders were weighed again on the same day, any storage band present was removed and they were then provided with the alternate feeding treatment for another seven days. The storage bands and the spiders were measured on Day 8 of the alternate treatment. Thus, each spider experienced a low-density and a high-density feeding treatment. We used paired parametric and non-parametric tests to examine the difference in spider weight and size of food storage before and after the paired treatments.

Prey encounter rates and food hoarding in N. edulis

Here we tested the influence of varying prey-encounter rates on the storage behaviour of *N. edulis*. Accordingly, spiders that receive food at constant rates may ingest the food immediately and store less externally than those that encounter food at variable rates, where excess food may be stored externally. We designed two experiments that varied in the difference between constant and variable prey-encounter rates. In both experiments, the mean prey-encounter rate was the same in each treatment.

In the first experiment, spiders were provided with two flies per day for 15 days in the constant treatment, and six flies every third day for 15 days in the variable treatment. After 15 days, the treatments were reversed and continued for another 15 days. Spiders were weighed and the storage bands removed and their length measured before and after each 15-day treatment. We used paired *t*-tests to examine the effect of prey-encounter rate and spider weight on storage behaviour. In the second experiment, spiders in the constant treatment were provided with four flies every day for nine days and 12 flies or no flies at a random order (from Day 1 to Day 9: 12, 12, 0, 0, 12, 0, 0, 0, 0) in the variable treatment. These treatments were not reversed, as the spiders became highly satiated. Spiders were weighed the day before the treatment

commenced and the day after the treatments finished. The length of the storage bands was measured on Day 10, and analysed with *t*-tests.

Food storage and the size and species of prey in N. edulis

Here we investigated whether spiders store prey selectively according to their type and size. We identified three different fates for prey: stored in the web, discarded (dropped to the floor) or consumed entirely. Almost all prey offered were attacked by the spiders. Females were placed in clean frames and each individual was fed two prey types: a single blowfly or a single cricket in random order, with 24 h between the feeding events. The prey was weighed several hours before being fed to the spider and the fate of each item was recorded the following day. The prey remains (whether stored or discarded) were dried in an oven (180°C for 30 min) and weighed to calculate the proportion of prey ingested. The frequencies of flies and crickets that were stored, discarded or consumed were analysed using Chi-square tests.

Effects of storage-band removal on N. edulis and N. plumipes in the field

N. edulis was observed under natural conditions in Euroa during February 2001. The following parameters were recorded: number of kleptoparasites present, female weight and storage size (length). The influence of food storage on future storage behaviour was investigated by removing the storage band from the webs of a random subset of *N. edulis*. The control group suffered a similar disturbance to the web but without removal of the storage band. We measured the size (length) of the storage after seven days to estimate size increase in the storage band.

Adults of *N. plumipes* were observed under natural conditions during March 2001 in West Pymble Park. We marked 80 adult female *N. plumipes*, and allocated them to one of four treatments. Treatment 1 had the food storage and all kleptoparasites removed every day; Treatment 2 had only the kleptoparasites removed each day; Treatment 3 had the food storage removed each day but the kleptoparasites were not removed; and Treatment 4 retained the food storage and natural densities of kleptoparasites, but were exposed to similar treatment disturbance. These treatments were maintained for seven days and we monitored daily the number of kleptoparasites, the size of the food storage, and the prey-capture rates. All spiders were weighed on Day 7 and the vertical and horizontal web diameters were measured at the start and at the end of the experimental period. Web size was estimated by multiplying the horizontal radius by the vertical web radius.

Antipredator function of the storage band in N. plumipes

We conducted a removal experiment in the field during April/May 2001 in West Pymble Park. In total, 60 adult female *N. plumipes* were selected, and their tibia patella length (first leg) and abdomen width were measured using callipers. After being marked individually with bee tags, the spiders were randomly allocated to two treatments: spiders in the experimental treatment had the storage band removed, whereas spiders in the control treatment were similarly disturbed without removing the storage band. Each spider was monitored daily for four weeks and we noted if any individual moved web site, was found dead in the web or disappeared altogether. Any storage bands constructed subsequently by the removal group were excised. We predict that if these bands function to deter predators, spiders whose storage bands were removed would suffer higher rates of mortality than those that retained the bands.

Analysis

We used a Kolmogorov–Smirnov test for normal distribution. All data that were not normally distributed were log-transformed and, if appropriate, analysed using parametric tests. Data that were still non-normal after transformation were analysed using non-parametric tests. All data are expressed as mean \pm s.e.

Results

Natural history of the storage band

Analysis of the content of the storage bands (length = 12.5 ± 1.53 cm, $n = 28$) in the webs of *N. edulis* showed that approximately 35% of the stored material consisted of plant matter such as small sticks, leaves and seeds. The remaining 65% consisted of prey remains. The storage bands of *N. plumipes* (length = 3.36 ± 0.38 cm, $n = 57$) were different in shape and

composition from those of *N. edulis*. There were no plant parts incorporated and the pieces of prey were not as densely packed as in those of *N. edulis*.

Prey density and food hoarding in N. edulis

There was no significant difference in the initial weights between spiders that first experienced the low (0.51 ± 0.052 g) and the high (0.53 ± 0.048 g) prey-density treatments (paired *t*-test: $t_{19} = -0.82$, $P = 0.42$). However, spiders did not gain weight when they experienced low prey density (0.51 ± 0.051 g; paired *t*-test: $t_{19} = 0.33$, $P = 0.73$), but did when they received prey at high densities (0.63 ± 0.058 g; paired *t*-test: $t_{19} = -2.46$, $P = 0.02$). Furthermore, when spiders captured more prey they also constructed larger storage bands (1.13 ± 0.2 cm) than when prey occurred at low densities (0.53 ± 0.14 cm; Wilcoxon signed ranks test: $z = 2.80$, $P = 0.005$).

Prey encounter rates and food hoarding in N. edulis

The final weight of spiders did not differ between the constant (0.54 ± 0.038 g) and slightly variable (0.54 ± 0.034 g) prey supply (paired *t*-test: $t_{20} = -0.15$, $P = 0.88$) treatment. Similarly, the length of the storage bands did not vary with the rate of prey encounter (paired *t*-test: $t_{20} = 0.92$, $P = 0.37$) (Fig. 1) when the contrast was low. When the contrast was high, spiders that received prey at a constant rate stored more food in the webs than did individuals that received prey at highly variable rates (*t*-test, $t_{37} = 2.46$, $P = 0.02$) (Fig. 1). There was no significant difference in the final weight of spiders in the constant (0.55 ± 0.04 g) and highly variable (0.67 ± 0.05 g) prey-supply treatments (*t*-test, $t_{37} = -1.62$, $P = 0.11$).

Prey size and species and food hoarding in N. edulis

Blowflies were more likely to be discarded and not stored in the web, while crickets were either stored in the web or completely consumed ($\chi^2_2 = 13.14$, $P < 0.01$) (Fig. 2). Even though flies (0.031 ± 0.002 g) were much smaller than crickets (0.15 ± 0.03 g), spiders ingested a higher proportion of the crickets (ANOVA: $F_{1,43} = 8.66$, $P = 0.005$) (Table 1).

Effects of storage-band removal on N. edulis and N. plumipes in the field

There was a significant difference in the initial weight of *N. edulis* spiders between the removal (1.60 ± 0.15 g) and the control (1.17 ± 0.16 g) group (*t*-test: $t_{21} = 2.15$, $P = 0.04$)

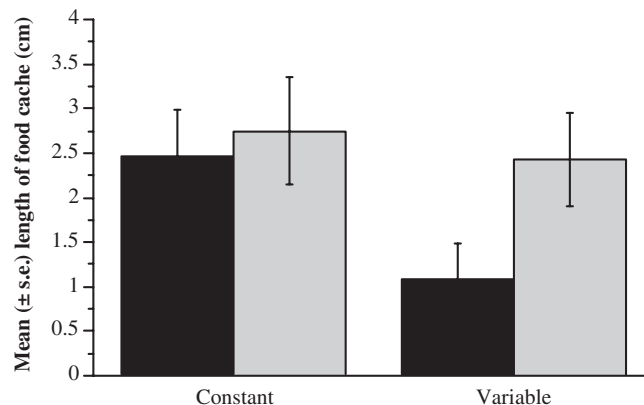


Fig. 1. Cache size in *N. edulis* under constant and variable feeding treatments. High contrast: black columns; low contrast: grey columns

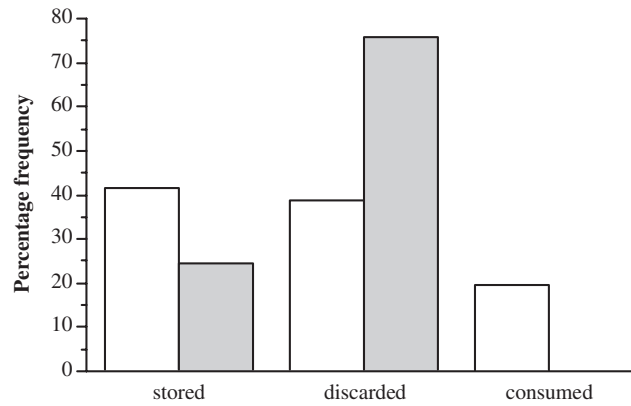


Fig. 2. Percentage of prey that was stored in the web of *N. edulis*, discarded or consumed. Crickets: white columns; flies: grey columns.

Table 1. The weight (g) of prey remains (flies or crickets) that were either stored in the web of *N. edulis* or discarded and dropped to the floor

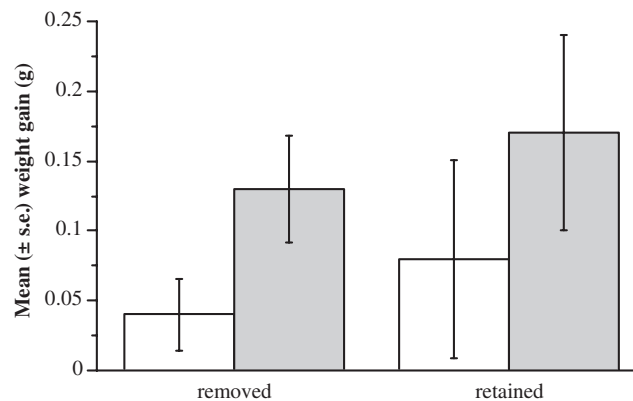
Prey	Fate	Mean \pm s.e.	n
Fly	Stored	0.1 \pm 0.02 g	9
	Discarded	0.07 \pm 0.16 g	18
Cricket	Stored	0.04 \pm 0.02 g	12
	Discarded	0.02 \pm 0.02 g	8

despite random allocation of individuals to each treatment. Thus, initial weight was used as a covariate in subsequent analyses. The absence (weight gain: 0.24 ± 0.05 g) or presence (weight gain: 0.17 ± 0.04 g) of a food store did not affect weight gain (ANCOVA: $F_{1,22} = 1.75$, $P = 0.2$). However, spiders whose storage bands had been removed incorporated more material (4.95 ± 1.5 cm over 7 days) into a new band than did the control spiders (0.92 ± 0.3 cm over 7 days) (ANCOVA: $F_{1,22} = 7.59$, $P = 0.01$). Thus, in *N. edulis*, the length of the storage band after the experiment did not differ between the two groups (ANCOVA: $F_{1,24} = 0.001$, $P = 0.97$). The webs of *N. edulis* were host to few kleptoparasites (only 5 of 35 surveyed webs). By contrast, 53 of 62 webs of *N. plumipes* contained the kleptoparasite *Argyrodes antipodiana*. Thus we examined the effect of food storing on kleptoparasite activity only in *N. plumipes*.

Across all treatments, larger *N. plumipes* built larger webs ($r = 0.65$, $n = 49$, $P = 0.0001$), more prey was captured in larger webs ($r = 0.42$, $n = 49$, $P = 0.003$), and larger females stored more food than smaller females ($r = 0.35$, $n = 49$, $P = 0.014$). The initial weight of spiders differed significantly between treatments (ANOVA: $F_{3,48} = 5.10$, $P = 0.004$) (Table 2), and initial weight was used as a covariate in subsequent analyses. The weight of spiders at the end of the experiment did not differ between treatments (ANCOVA: $F_{3,48} = 2.40$, $P = 0.08$) (Table 2). In contrast to those of *N. edulis*, food stores in *N. plumipes* did not grow as rapidly in the removal group. Consequently, the length of the storage band at the end of the experiment differed significantly between the removal (1.14 ± 0.39 cm) and control (1.85 ± 0.37 cm) group (ANCOVA: $F_{1,62} = 23.40$, $P = 0.0001$). Weight gain of females over the seven experimental days (Fig. 3) was not influenced by the presence of the

Table 2. The mean (\pm s.e.) initial weight (g) of *N. plumipes* randomly allocated to four experimental treatments

Group	Cache	Kleptoparasites	Initial weight	Final weight	<i>n</i>
1	Removed	Removed	0.40 ± 0.09 g	0.53 ± 0.11 g	9
2	Retained	Removed	0.46 ± 0.1 g	0.62 ± 0.15 g	11
3	Removed	Retained	0.61 ± 0.09 g	0.65 ± 0.08 g	14
4	Retained	Retained	0.82 ± 0.08 g	0.70 ± 0.05 g	15

**Fig. 3.** Weight gain of *N. plumipes* where the food cache had been removed or retained. White columns: kleptoparasites removed; grey columns: kleptoparasites retained.

storage band (ANCOVA: $F_{1,48} = 0.32$, $P = 0.58$), the presence of kleptoparasites (ANCOVA: $F_{1,48} = 2.30$, $P = 0.14$) or the interaction of these two factors (ANCOVA: $F_{1,48} = 0.001$, $P = 0.98$).

Antipredator function of the storage band in *N. plumipes*

There was no significant size (tibia–patella length) difference between spiders in the control (1.17 ± 0.27 cm) and removal (1.16 ± 0.36 cm) treatments (t -test: $t_{58} = 0.22$, $P = 0.83$). Furthermore, the condition of spiders in both treatments (calculated as the standardised residuals generated by the regression of abdomen width on tibia–patella length) was similar (t -test: $t_{58} = -0.14$, $P = 0.89$). Contrary to prediction, spiders on webs without storage bands did not suffer higher rates of mortality: 15 of 30 individuals in the removal group and 15 of 30 individuals in the control group died or disappeared (Yates-corrected $\chi^2_{1} = 0.07$, $P = 0.8$).

Discussion

Our experiments clearly showed that variation in hoarding behaviour in *Nephila* can be attributed to prey density, prey encounter rates and prey type. Nevertheless, removal experiments of external caches in the field were unable to detect changes in weight gain or an influence of kleptoparasites. Furthermore, spider mortality was unaffected by the absence or presence of the storage band.

Food hoarding is advantageous if it allows the animal to capitalise on temporarily abundant food resources and/or decreases foraging activities when costs, such as exposure

to predators, are high (Sherry 1985). Accordingly, we found that *N. edulis* stored more prey externally when prey was abundant than when it was limited. The established caches may be accessed when the animal has high energy requirements, such as during the final stages of an egg sac formation. Furthermore, the externally stored prey may allow the spider to process the prey at a later stage if they are physiologically limited by the amount of food they can ingest at any one time or if internal fat stores reduce mobility. Spiders are able to ingest a large amount of food at any time due to the presence of gut diverticula (Foelix 1992).

For most food-storing birds and mammals, a good spatial memory is often essential for retrieving the cache (e.g. Herz *et al.* 1994), but this is unlikely to limit cache relocation in *Nephila*, because the cache is located in the web. Moreover, the close proximity to the cache may also allow the spider to defend the cache from pilfering, a common cost of storing food externally (e.g. Leaver and Daly 2001).

Animals not only respond to food density, but also to variation associated with the food resource (Caraco 1981; Caraco and Gillespie 1986; Kalcenik and Bateson 1996; Herberstein *et al.* 2000b). Here, variation in prey encounter affected storage behaviour when the contrast between the treatments was high: spiders tended to store more food under constant prey supply than under variable rates. These patterns are consistent with those of other food-hoarders: for example, unpredictable food supply to starlings (*Sturnus vulgaris*) results in greater mass gain due to internal fat storage (Cuthill *et al.* 2000). Similarly, tufted titmice (*Parus bicolor*) do not increase their rate of food caching under unpredictable food regimes but rather increase their internal fat stores (Pravosudov and Grubb 1997). However, in these studies, food hoarding reflects the necessity to maintain high body temperature in cold nights without food (McNamara and Houston 1990; Pravosudov and Grubb 1997). In spiders, food hoarding is unlikely to be based on the same proximate mechanism. Thus the variation in caching in *N. edulis* may not reflect energy balance *per se* but the relative cost of cache loss, which may vary in different prey environments: when prey-encounter rates are constant, the cost of cache loss may be relatively low. In contrast, under unpredictable encounter rates loss of the external storage may be higher, if a period of food shortage follows. Under such prey conditions, the relative benefits of internal storage may be greater.

Food hoarding is adaptive if the individual can retrieve the cache under periods of food shortage or high energy requirements (Andersson and Krebs 1978). Removal of the cache did not affect weight gain in natural populations of *N. edulis* and *N. plumipes*. Perhaps our experiments were not sufficiently long to incorporate temporal changes in food availability, and hence detect the differences obtained in the laboratory experiments. Interestingly, removal of the cache did not affect the density of the kleptoparasite *A. antipodiana* in the webs of *N. plumipes*. Similarly, weight gain in *N. plumipes* was not influenced by the abundance of kleptoparasites. These data suggest that *A. antipodiana* do not significantly impact on the nutrients available in the cache, perhaps preferring to feed on those prey items ignored by the host spider (Cangialosi 1990; but see Whitehouse 1997; Tso and Severinghaus 1998). Nevertheless, it is tempting to infer that the relatively high abundance of kleptoparasites on the webs of *N. plumipes* (see also Elgar 1989) compared with *N. edulis* is responsible for the relatively large food cache that is typical of *N. edulis*. Such large food caches may attract extremely large numbers of kleptoparasites in *N. plumipes*.

The value of an external cache depends, in part, on the future value of the stored items. Food may improve during storage (e.g. ripen) or perish through microbial activity (Gendron and Reichman 1995). Consequently, not all food items are suitable for long-term caching (Reichman 1988). Nevertheless, by modifying food items, storability can be increased (e.g.

Fox 1982; Reichman *et al.* 1986). Our laboratory experiments similarly suggest that not all prey types are suitable for storage in *Nephila*. The remains of blowflies were discarded more frequently than stored and never consumed completely. In contrast, crickets were stored externally or consumed entirely, even though the crickets were a much larger meal than the flies. Thus, crickets may be more suitable for external and internal storage than flies. Alternatively, flies may contain more indigestible exoskeleton than crickets and are therefore never consumed entirely.

The storage bands of *N. edulis* in the field include about 35% plant material, while those of *N. plumipes* contain only animal material, even though plant material was available. This difference is intriguing and suggests that the storage band may serve other functions for *N. edulis*. For example, decomposing plant and animal material may attract insects to the web, thus increasing the spider's foraging success. However, the rate of decomposition appears to be very slow, and was not obvious throughout the study. Alternatively, the storage bands may deflect predators from the spider by acting as a decoy, thereby confusing the predator (Hingston 1927; Edmunds and Edmunds 1986; and see Herberstein *et al.* 2000a for a review). However, our field experiment found no mortality effect upon the removal of the storage band in *N. plumipes*.

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