

**PREDATORY PLASTICITY IN NEPHILENGYS CRUENTATA
(ARANEAE: TETRAGNATHIDAE): RELEVANCE FOR
PHYLOGENY RECONSTRUCTION**

by

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Summary

The plasticity of behavioural expression has been used as an argument against the use of behavioural characters in the reconstruction of phylogenetic patterns. Nevertheless, plasticity itself may vary strongly among taxa, so that phylogenetic considerations about behavioural data must be complemented by an analysis of behavioural plasticity. Plasticity may also vary among distinct behavioural domains in a single species. We have studied the foraging repertoire in *N. cruentata* using a cluster analysis method, in order to identify the behavioural sequences employed by the spider when preying upon either distinct prey types or distinct prey sizes. Foraging behaviour varies less with prey size than with prey type. Variation in predatory sequences is obtained through (1) repetitions of one same sequence of categories, (2) the use of one same sequence at distinct phases of the predatory behaviour, or (3) the arrangement of behavioural categories in new sequences. Despite this plasticity in spider responses to prey, almost 40% of the predatory repertoire is common to both large and small prey items; this percentage lowers to 20% when we compare the predation of distinct prey types. These results suggest that phylogenetic analysis of predatory behaviour should focus on building ethograms for one single prey type. Small variations in prey/predator size among the predator species selected for a behavioural phylogenetic analysis are preferred to variations of prey type among predator taxa. We discuss the implications of this 'single prey-type' approach to the phylogenetic analysis of behaviour.

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Introduction

The lability of behavioural expression has been used as an argument against the employment of behavioural characters in the reconstruction of phylogenetic patterns (Atz, 1970; Urbani, 1989; Greene, 1994; but see de Pinna, 1997). Indeed, behaviour varies not only as a function of environmental factors (see review in Wcislo, 1989; for more recent articles, see Malcolm, 1989; Mousseau & Dingle, 1991; Groothuis, 1993; Costa & Sotelo, 1994; Pasquet *et al.*, 1994; Li & Jackson, 1996; Roland *et al.*, 1996), but also of experience and/or learning (for example, Marler, 1970; Jackson & Wilcox, 1993; Edwards & Jackson, 1994). According to this line of reasoning, behaviour is so inextricably tied to environmental factors, that it actually reflects these factors more closely than any endogenous organization, so that it should not be taken as a reliable source of information on evolutionary history (but see Wenzel, 1992 for a criticism of the endogenous-exogenous dichotomy).

If behaviour is, in any special way, linked to present environmental features, it should exhibit a high level of homoplasy in phylogenies. Nevertheless studies utilizing phylogenetic systematic methodology have indicated that stereotyped behavioural characters are as useful in reconstructing phylogenetic relationships as morphological and molecular traits (McLennan *et al.*, 1988; Prum, 1990; De Queiroz & Wimberger, 1993; Paterson *et al.*, 1995; Slikas, 1998), and some authors have even showed that behavioural characters perform better than morphological ones in phylogenetic analyses (Scharff & Coddington, 1997).

If, at one side, stereotypic behaviour is useful to the reconstruction of phylogenetic relationships, at the other side, the plastic aspects of behaviour are yet underexplored in this context. The level of plasticity in behaviour varies strongly among taxa: it is clear, for example, that learning capabilities are not equally distributed among such disparate groups as primates, insects, birds and annelids. Even within one same group, plasticity may vary strongly. Spiders, for example, may use specialized predatory strategies for the capture of certain prey taxa (Robinson & Olazarri, 1971; Coddington & Sobrevila, 1987; Edwards & Jackson, 1993), but may also learn how to capture their prey items (Jackson & Wilcox, 1993; Jackson & Pollard, 1996) or may

show flexibility in other aspects of their behaviour (Eberhard, 1988). Thus, an important issue that needs to be addressed now is whether there is any phylogenetic signal in those aspects which contribute to the impression that behaviour is 'flexible'.

In this paper we evaluate behavioural plasticity in the spider *Nephilengys cruentata* (Araneae, Tetragnathidae), in its foraging aspects, focusing not on stereotyped, simple units of behaviour, but rather on higher order routines, on the linear arrangement of these behavioural units. We know a fair amount about the behaviour of this giant orbweaver; she changes web pattern throughout development (Japyassú & Ades, 1998) and aspects of the microhabitat may influence the timing and course of this developmental change (Japyassú & Ades, in prep.); mechanisms of conspecific attraction and selective site desertion help maintain a clumped habitat distribution (Schuck-Paim & Alonso, in press); at this level of aggregation, it is not surprising that competition for web site exists among conspecifics (Santos-Filho, subm.). In the present research we dissect this spider's behavioural plasticity by means of two experiments, trying to distinguish between prey-kind and prey-size induced changes in the predatory repertoire. We also discuss the relevance of the results, and of plasticity in behavioural repertoires in general, to the use of behavioural data in the reconstruction of phylogenies.

Methods

The predatory sequence of *N. cruentata* preying upon the larvae of the beetle *Tenebrio molitor*, the cricket *Gryllobates sigilattus*, and the fly *Musca domestica* was tape-recorded under natural conditions (outside buildings at Butantan Institute and University of São Paulo, SP, Brazil).

In order to evaluate the influence of prey size on the behavioural sequence, we offered 3 sizes of *T. molitor* beetle larvae to adult female spiders: in one group, the spiders were larger than the prey ($S > P$; $N = 10$), in the other prey/predator sizes were similar ($S = P$; $N = 10$) and in the last one spiders were smaller than the prey items ($S < P$; $N = 10$).

In a second experiment the adult female spiders captured *M. domestica* flies ($N = 10$), *T. molitor* larvae ($N = 13$) and small ($N = 15$) or large ($N = 19$) *G. sigilattus* crickets.

Each spider captured only one prey item and was observed only once. The behavioural sequences were tape recorded, and recording was stopped at the end of the predatory sequence (*i.e.* after a 1 min long bite at the hub/retreat) or after any 5 min interruption (pause) in between the sequence.

Behavioural repertoire

The basic behavioural categories are described elsewhere (Robinson & Olazarri, 1971; Viera, 1983, 1986, 1994). Some new behavioural categories are herein described (or those somewhat different from available descriptions), based on preliminary observations of the spider's predatory sequence upon diverse prey items.

Web-plucking: the spider runs towards the prey, halts motion and tightens the front radii with legs I and/or II. This is used before prey capture, seemingly as a way of locating the prey.

Pluck-out-prey: with a sustained long-bite at the periphery of the web, the spider stretches out legs I and II (clasped to radii), trying to untangle the prey from the capture web. As a rule this behaviour is repeated many times until the prey is freed from the web; if that does not happen, the spider usually initiates a wrapping bout.

Prey-carrying: there are some variants of this behaviour. The prey can be transported to the hub either by the jaws (for example, after a successful pluck-out-prey) or hanging from the spinnerets, with leg IV grasping the prey or the line fixed to it (if the prey was wrapped at the periphery of the web). In the first case, the spider usually returns by the guide-line; in the latter, she usually returns walking via the capture web.

Line-laying: at the hub, with the prey hanging from the spinnerets, the spider extends the fourth leg which is grasping the prey so that the distance between the wrapped food and the spider enhances; this movement can be repeated once or twice.

Store-at-hub: after line-laying the spider fixes several times at the hub/retreat while rotating its body sagittally in order to face the prey.

Self-grooming: the spider chews its legs smoothly as they pass slowly and individually through the jaws. Alternatively the spider can rub one leg against each other repeatedly. This usually happens after prey immobilization, at the hub/retreat.

Other behavioural categories used to describe prey capture were: rotate-at-hub; two stepwise approaches (one from retreat to hub, the other from hub to prey), short and long-bites, silk-attach, silk-cut, pause, touch-prey, wrap, prey-retrieve, prey-handling and other-displacements.

Analysis of behavioural sequences

The behavioural sequences in each treatment group were transformed into a preceding-following acts transition matrix (one per group). In order to detect the most probable behavioural sequences in each treatment group, we used the Direct Tree method (see Christofides, 1975) on each transition matrix. This algorithm produces a hierarchical representation (DiTree) with all behavioural categories in the matrix placed as nodes in a branching diagram, whose base is called a root. Each matrix results in as many DiTrees as the number of behavioural categories included in it, each DiTree with a distinct category taken as its root. After selecting the root, the DiTree algorithm searches for the tree that maximizes the sum of the transition probabilities between all the behavioural categories, which means that the sequences therein are the most likely to occur given that root and data set.

Following Alberts (1996), each DiTree was decomposed in its branches, that is, the multiple linear sequences of behavioural categories from the root to each final leaf of the diagram. The linear sequences which occurred in the original tape-recorded data were called 'behavioural routes', and their incidence was compared among the treatment groups.

Statistical analysis

Due to small sample sizes and to the departure from normality in the frequency of some behavioural categories, we used non-parametric statistical tests.

To evaluate capture success among different prey size groups we used Kruskal Wallis 1-way Anova. For the remaining analyses only data from successful capture attempts were used. Since spiders smaller than prey showed small success in prey capture (2 out of 10 attempts) we combined the results from two treatments, yielding two combined groups: Spider \leq Prey ($N = 11$) and S $>$ P ($N = 10$).

If there was a difference between the experimental treatments, a Canonical Discriminant analysis was used to detect the behavioural categories which most contribute to this differentiation. Each behavioural category entered the analysis in a stepwise mode, with $F = 0.05$ to enter and $F = 0.10$ to remove from the discriminating functions; the rule to select between available behavioural categories was to minimize Wilks' Lambda. Prior probabilities for individual cases were computed from group size.

Results

During the preliminary observations in the categorization phase of the study we observed spiders approaching large crickets without trying to bite them after the first contact. The spider touches the cricket, cuts web threads just above it and simultaneously fixes several lines to the margin of the preserved part of the web, knitting together the severed border just above the prey. At first we thought that the spider was rejecting the prey, trying to throw it out of the web. But later we realized that this cut-above sequence resulted in a loosening of the lower part of the web, making it more stretchable, and thus less vulnerable to the preys' kicks. This strategy also collapsed web radii and spirals upon the prey, which became more effectively entangled. The cut-above/bite/wrap procedure represents a third capture technique, joining the known araneid bite/wrap and theridiid wrap/bite sequences; this rare strategy was observed only twice during the preliminary observations.

Capturing different sized prey in distinct ways

As prey become larger in relation to spider size, there is an increase in the spider behavioural investment, *i.e.* there is an increase in the number of behavioural categories employed in a successful capture (Fig. 1, $N = 21$; Mann-Whitney $U = 2$; $p < 0.001$). The first contact with prey becomes more elaborate and the attempts to immobilize it involve multiple short and/or long bites, and various wrapping events.

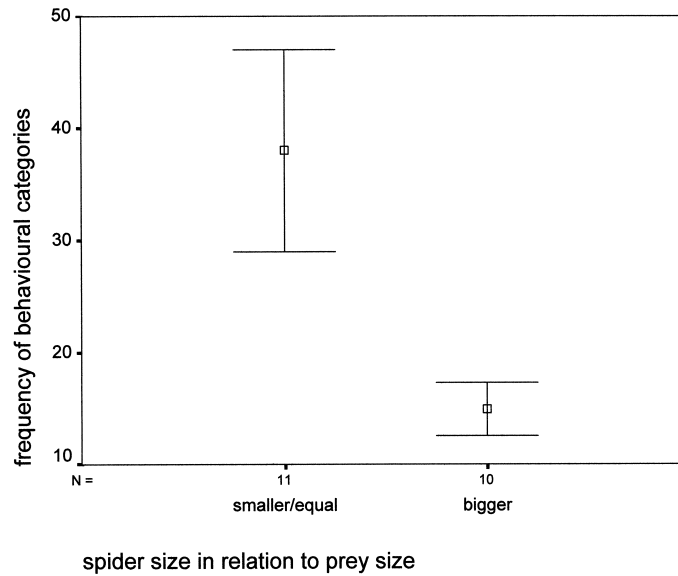


Fig. 1. Overall frequency of behavioural categories employed in successful prey captures. As relative spider size diminishes, the behavioural costs of prey capture increases.

In order to describe quantitatively the behavioural differences between prey size groups, we performed a canonical discriminant analysis, which yielded two discriminant functions. The first category to enter the analysis was prey wrapping, which is the main contributor to function 1 in the canonical discriminant analysis; as the relative size of the spider decreases, the frequency of prey wrapping bouts increases. As this first canonical function accounts for 86% of the variance between groups, changes in the frequency of prey wrapping bouts is by far the main behavioural modification that results from changes in the relative size between spider and prey.

The appearance of wrapping behaviour in the prey capture sequence also varies in relation to prey size: small prey items are carried to the hub in the jaws and there they are wrapped (Fig. 2); larger items are wrapped at the capture site and carried to the hub hanging from the spinnerets (Fig. 3). The capture of larger items requires an increase in the frequency of some other behavioural categories: short bites during prey immobilization, silk cutting while wrapping the prey, pauses scattered along the sequence and also self-grooming before retrieving the prey.

Notwithstanding the enhanced prey capture efforts, spiders succeed less frequently as prey become larger ($N = 30$; $\chi^2 = 8.2857$; $p = 0.0159$).

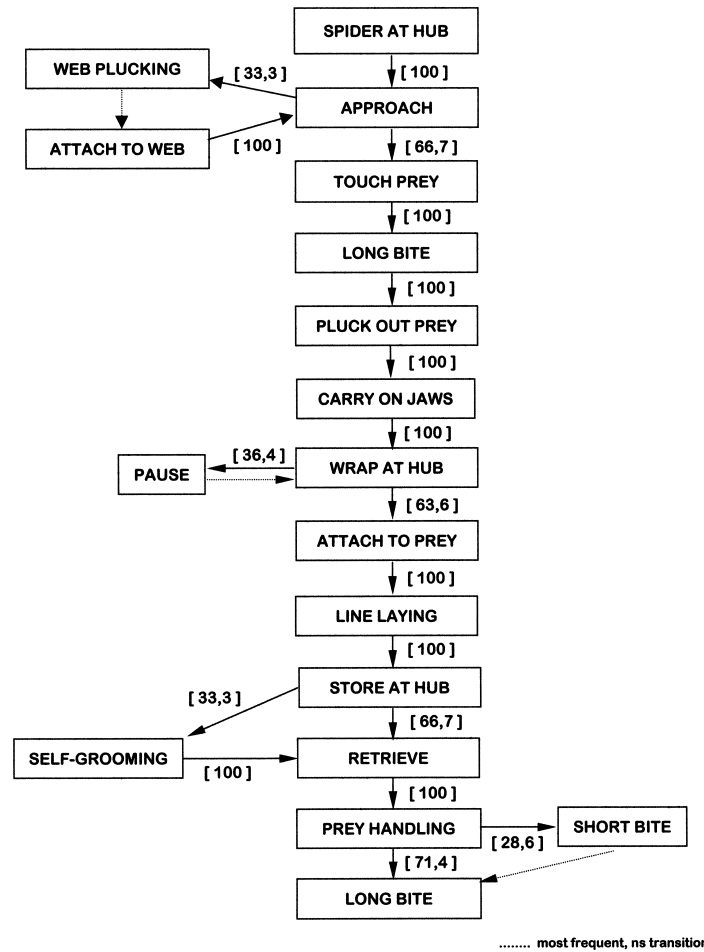
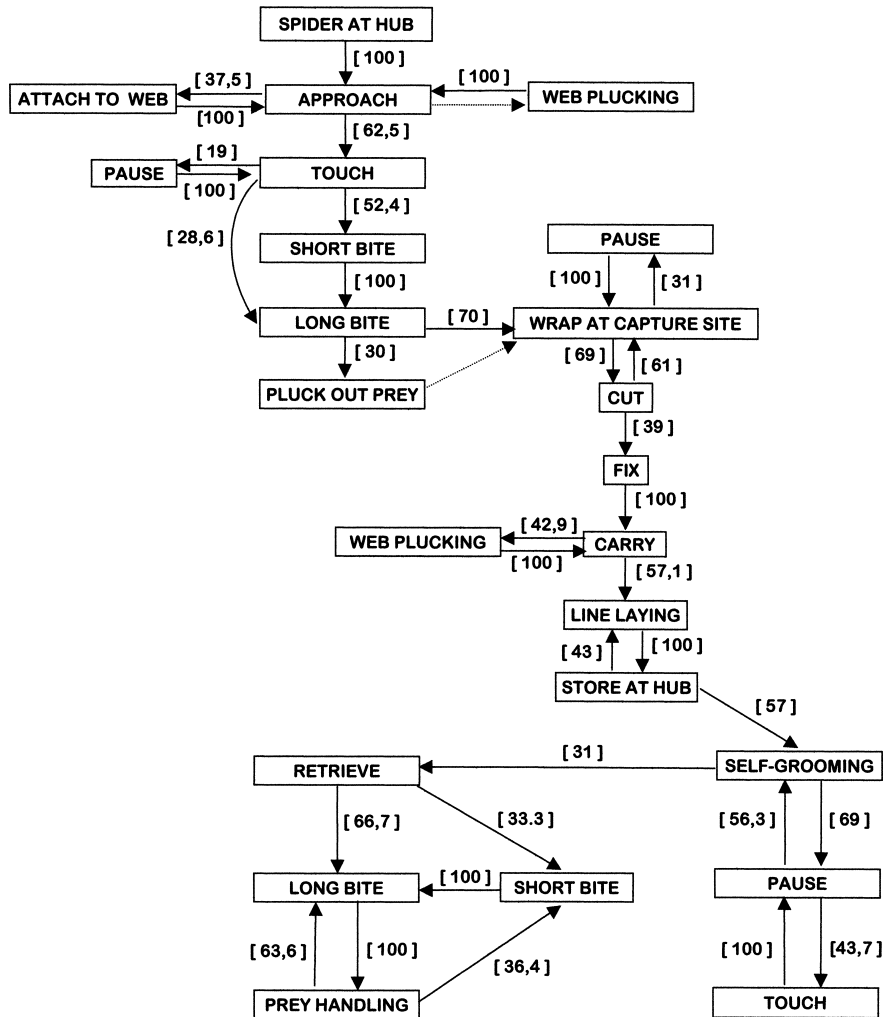


Fig. 2. Ethogram of *N. cruentata*'s predatory sequence upon small beetle larvae.

Although the benefits increase with prey size, the risks of an unrewarded investment also grow, so that there must be a compromise between the costs and the advantages of these capture attempts. This compromise could explain the high number of spiders that show no reaction to large prey items; the investment might be too risky to be worthwhile.

Capturing different sized preys in a similar way

Although the behavioural sequences vary as a function of prey size, still there is considerable overlap among them. The DirectTree method yielded



..... most frequent, ns transition

Fig. 3. Ethogram of *N. cruentata*'s predatory sequence upon large beetle larvae.

219 distinct behavioural routes, 86 common to the Spider > Prey and Spider ≤ Prey groups (almost 40% similarity: Table 1).

These shared behavioural routes do not necessarily appear at the same phase of the capture sequence, nor in the same behavioural context. For example, the sequence approach/touch/short-bite appears during the immobi-

TABLE 1. *Communality of behavioural routes among prey sizes and types (%)*

	larvae \geq spider	beetle larvae	small cricket	large cricket
fly		4.76	7.48	5.93
beetle larvae			19.47	22.73
small cricket				27.15
larvae < spider	39.27			

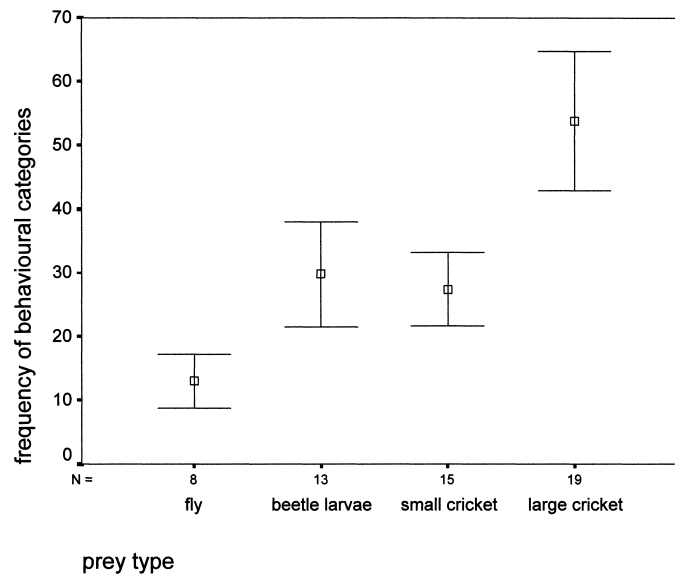


Fig. 4. There is an overall change in the frequency of behavioural categories with prey type. This difference is not significant when comparing same-size prey types (beetle larvae and small crickets).

lization phase in the capture of small prey items, while it appears immediately before ingestion at the hub in the capture of large prey items.

Capturing distinct prey taxa

Changes in prey taxa offered to the spider lead to strong (Fig. 4), significant changes in the frequency of events in the capture sequence ($N = 55$; $\chi^2 = 30.819$; $p < 0.001$). These changes may be due to both taxonomic and size differences between the prey items offered. To control for size

influences, we compared the spider behaviour when preying upon distinct taxa of comparable size (tenebrio larvae and small crickets). There was no difference between the capture of these prey taxa ($N = 28$; Mann-Whitney $U = 92.5$; $p = 0.821$); small cricket and tenebrio larvae are captured with the same behavioural categories, in the same frequency.

Although distinct same-size prey taxa are captured with equal frequency of behavioural categories, there may still be differences in the sequence of categories. The DiTree method resulted in 710 distinct behavioural routes: 239 with large crickets, 234 with small crickets, 221 with beetle larvae and 155 with flies. Only three routes (0.42%) were common to all prey taxa: attach-to-prey/silk-cut, touch/prey-handling and short-bite/long-bite/pluck-out-prey. These are basic behavioural sequences, almost invariants, since they occur in all such disparate conditions. Within the same prey size class there is almost 20% similarity between predatory sequences (74 out of 380 behavioural routes for small cricket and tenebrio larvae: Table 1).

Discussion

As expected, our results demonstrate the existence of a strong plasticity in *N. cruentata*'s predatory behaviour. The spider varies its behaviour according to prey size and kind. This is not at all surprising, since spiders are well known generalist and opportunist predators (Wise, 1993; Foelix, 1996): they must be flexible in order to cope with the immense variability of naturally occurring prey. Predatory behaviour must be at least partially guided by external cues in order to be successful.

Nevertheless, plasticity is not uniform among experimental treatments. Prey-size changes entail less modifications than prey-type changes. In fact, an unexpectedly large number of behavioural routes do not vary as a function of prey size (86 out of 219); a smaller number of behavioural routes are conserved when the spider preys upon similar sized beetle larvae and crickets.

Unravelling behavioural plasticity

The analysis of the capture sequence shows in detail the various levels of behavioural plasticity. The first is a very low level plasticity, one that is the result of a simple feedback mechanism that functions on and on

until the desired prey state is obtained. Many more wrapping bouts are necessary to capture a large larvae than a small one. Consequently, there is an extraordinary increase in the frequency of wrapping and other associated behavioural categories (such as silk-cut and fix, prey-touch and bite), but there is no new behavioural route involved. The first level of predatory plasticity is thus the repetition of behavioural routes until some desired state of the prey is obtained.

Changes in prey size may entail huge changes in the topology of the ethogram (compare Figs 2 and 3). What seems to be an extraordinary innovation, however, is mainly the result of changes in the timing of behavioural routes (for example, the wrapping sequence occurring during either the ingestion [Fig. 2] or the immobilization [Fig. 3] phase). This shows another level of plasticity: a reordering of behavioural routes along the predatory sequence. With this reordering the same behavioural sequence can be used in different contexts, *i.e.* it can serve different functions.

The last aspect of behavioural plasticity involves the use of completely new behavioural routes. This happens mainly (but not exclusively) when we change prey type: more than 80% of the behavioural routes employed in the capture of tenebrio larvae were not used in the capture of small crickets (Table 1). Different prey types, with their new kinds of movements, elicit novel sequences, which are incorporated into the flow of the spider's behaviour.

Our analysis demonstrates that 'plasticity' may have many meanings: routine repetition in a feedback loop, the use of the same routines in different contexts, and finally the use of new routines. It is not clear that plasticity is the manifestation of the same underlying mechanism in all these cases. For example, does prior experience with prey affect all of these manifestations of plasticity equally? Prior to the study of the evolution of plasticity, it is desirable to refine the study of plasticity itself, to avoid confusing different levels of analysis.

Contributions to the study of the evolution of predatory behaviour

Besides web morphological characters (presence or absence of some web structures), the use of behavioural characters for the reconstruction of spider phylogeny has until now been restricted to details of spider performance, such as the use of a particular leg at a specific moment of web construction,

or the method of subduing prey (for detailed examples, see Eberhard, 1982; for recent utilization of such characters, see Scharff & Coddington, 1997; Griswold *et al.*, 1998). Although this is a successful approach, it does not encompass the great variability for which behaviour is well known, focusing on stereotyped details of performance.

The behavioural routes method employed in this paper allows the sampling of a variety of behavioural sequences, thus recovering much of the inherent variability of behaviour. Due to this recovering of behavioural variability we suggest the behavioural routes method as a complementary approach, one which provides additional characters to phylogeny reconstruction, and one that is particularly suited to study the evolution of the plastic aspects of performance. Each behavioural route, that is, each linear sequence of stereotyped behavioural categories (which follow each other with varying probabilities) may be considered a new character in a phylogenetic matrix. Alternatively, a group of behavioural routes which partially overlap with one another (which have partial sequences of categories in common with one another) could be scored as one single character. In this case this character would be defined by the common, underlying sequence (for example, short-bite/long-bite/pluck-out-prey), plus a variation (the other categories which may occur before or after the main sequence).

The analysis of behavioural sequences requires a huge data collecting effort, and this effort is even greater when many species have to be compared. Plasticity is, however, an inherent quality of behaviour, and it has been argued that it is a major factor in evolution (West-Eberhard, 1989; Pigliucci, 2001). Thus, if we rule out plastic behaviours from evolutionary studies, not only major aspects of animal behaviour (such as predation), but also an important quality of behaviour in general (plasticity itself), will be left aside.

We will attempt to demonstrate that even these plastic aspects of behaviour (such as foraging responses) can be reasonably accounted for in phylogenetic analysis. Since alterations in prey size and type induce changes in the spider predatory responses, a first solution to the phylogenetic analysis of predation would be to control for these factors across the terminal spider taxa. The use of one single prey species (with enough size variation to cope with size differences across the spider species included in the phylogenetic analysis) allows the reduction of the immense variability of foraging behaviour. With this 'single prey-type' approach to predatory behaviour we may

also reduce the data collecting effort to feasible amounts and gather comparable information among spider taxa.

Indeed, this solution is a way of narrowing plasticity: since behaviour is context-dependent, we can experimentally control the context, and thus analyse comparatively the evolution of behaviour *in that context*. This experimental control of context can be extended in many relevant aspects, such as the level of satiation of the spider or its previous experience with the chosen prey type.

Although the experimental control of context, as described above, facilitates the comparative study of plastic behaviour, it may be considered a somewhat Pirous' methodological victory, since this is a way to experimentally reduce plasticity until it becomes comparable among species. Some could argue that the main aspect of predatory behaviour is that it is a large repertoire of partial behavioural sequences (some elicited by one or another prey type, some others elicited in this or that context), so that this 'experimental control of context' is only a partial solution, one that allows the phylogenetic study of some behavioural sequences within the whole repertoire, and one that loses what is 'characteristic' of this kind of behaviour (that is, its plasticity).

Nevertheless, this 'whole repertoire' is something almost impossible to comprehend, since one can always think of new contexts in which the animal could present new behavioural strategies. The cut-above/bite/wrap subduing procedure described for the first time in this paper is an example of extreme variations in context (in this case, extreme prey/predator size differences) yielding new behavioural strategies. Thus, to obtain a 'whole repertoire' may be an unending task.

Also, if we are to understand behavioural evolution, there is no *a priori* benefit in comparing species' behaviour along multiple contexts: each context-dependent repertoire analysed across spider species should convey the same evolutionary signal, that is, should produce the same cladogram. This 'experimental control of context' approach allows an expansion of the study of behavioural evolution from the stereotyped to the plastic aspects of behaviour.

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