

Behavioural Plasticity in *Argyrodes antipodiana*

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ABSTRACT

In this thesis I look at the behavioural plasticity of *A. antipodiana* while foraging and interacting with conspecifics. The aim is to see how an animal, with apparently limited intelligence is able to deal with environmental variability. I conclude that *A. antipodiana* appears to have been able to overcome these limitations very effectively by using four methods, of which the first two effectively reduce the amount of learning necessary.

Firstly, *A. antipodiana* simplifies the situation as much as possible by ignoring some of the variability. For example, in social situations, *A. antipodiana* appears to recognize only a few categories of conspecifics, rather than recognize conspecifics as individuals. Consequently, the social groups of *A. antipodiana* are not characterized by complicating factors such as aggressive orders or dominance hierarchies.

Secondly, *A. antipodiana* largely ignores current situations and instead bases much of its behavioural decisions on its internal conditions. For example, in male-male conflicts, males respond to their opponents largely according to their own size, level of hunger, the number of contests in which they have participated, or their past experience of winning or losing; rather than to the characteristics of their opponents. Likewise in social interactions *A. antipodiana* is more inclined to be aggressive towards conspecifics if it itself is foraging, and less inclined if it is feeding with the host.

When the situation can not be simplified, *A. antipodiana* adopts a third response which is to use the simplest method possible for adjusting its behaviour. For example, *A. antipodiana's* ability to develop araneophagic skills appears to be governed by a critical period. Thus rather than developing araneophagic skills through trial and error with

practise, the ability appears to be simply 'switched on' if required.

The fourth means by which *A.antipodiana* compensates for limited intelligence is to be very selective in the areas in which it does use learning. For example, *A.antipodiana* seems to use problem solving when foraging, but only when it is actually trying to reach the foodbundle upon which the host is feeding. *A.antipodiana* also seems to learn to move more stealthfully on the host's web. There is even evidence that *A.antipodiana* may behave with intent when males are competing for opportunities to copulate.

Thus the intelligence of *A.antipodiana* appears to be severely limited. However, despite these limitations, by reducing the amount of learning necessary, and then channeling what learning it has to very restricted, but very poignant areas of its behaviour, *A.antipodiana*, is able to respond very effectively to its variable environment.

INTRODUCTION

What dictates the manner in which an animal behaves? Is behaviour predominantly instinctive, or must an animal learn most of its behaviour? Questions such as these have caused debates that have extended down through the centuries (Bolles 1988). During the 17th Century,

the common opinion was that there were innate principles which the soul received before birth (see Locke 1690). People 'learnt' by having this knowledge pointed out to them. Locke (1690) however, challenged this view and advocated that no knowledge is innate, and that all ideas come from sensation or reflection. Hence, he argued that we only learn from experience. Although this view was radical, it was difficult to challenge: people do seem to need to learn, for example, that 'a' causes 'b' - they do not seem to innately know that 'a' causes 'b'. Nevertheless, Hume (1738) did manage to challenge Locke's view by simply asking "why do we assume 'a' causes 'b'?" He pointed out that if 'a' happens before 'b', we assume that 'a' causes 'b'. Kant (1781) developed Hume's argument further and pointed out that the assumption of causality in humans is innate. That is, our mind innately uses cause and effect to arrange natural events. Thus he argued that the manner in which we think is innate. We modify our behaviour through learning, but what and how we learn appears to be governed by innate constraints.

This pattern of learning occurring within the boundaries of innate constraints is, perhaps, true in all animals. For example, it is unlikely that any animal is able to learn everything in all situations. Learning in every species is, perhaps, channeled in some manner, and presumably, it is more strongly channeled or restricted in animals with limited intelligence.

The ability to learn appears to be necessary in complex environments. In complex environments which change rapidly, an animal has not got 'time' to evolve appropriate innate responses. Often, the only means by which an animal, in such an environment, can develop an appropriate response is to learn that response (Johnston 1985). Thus an highly variable environment may place a heavy intellectual demand on an animal by requiring a lot of learning.

The aim of this thesis is to examine the means by which an animal with apparently limited intelligence is able to deal with environmental variability. In particular, emphasis is placed on the manner by which an animal channels or restricts its learning in order to use it most effectively.

To do this I looked at behavioural plasticity, learning and intelligence in the spider *Argyrodes antipodiana*. As *A. antipodiana* is a small invertebrate, it would appear to have limited intelligence. In addition, the environment in which *A. antipodiana* lives is highly complex and variable.

Unforeseen environmental variation is rife in the feeding biology of *A. antipodiana*, a small (3 mm long) silver spider that lives in small groups around the webs of larger spiders (Whitehouse 1986). *A. antipodiana* feeds by kleptoparasitizing a larger spider, which in New Zealand is mainly the orb weaver *Eriophora pustulosus* (Whitehouse 1988). *A. antipodiana* practices kleptoparasitism by moving down on to the 'host's' web and employing a range of foraging techniques. For example, it may glean small insects off the web or feed with the host. *A. antipodiana*, though, not only feeds with the host but also steals 'foodbundles' and may even eat the young of the host or eat the host itself when it has died while moulting (Whitehouse 1986). To perform this range of behaviours, *A. antipodiana* has to be successful at moving around undetected on the web of its host, a potential predator. An ability to adjust its behaviour to

its host's peculiarities would seem advantageous.

A. antipodiana's social organization is also complex. *A. antipodiana* form groups around the webs they kleptoparasitize, which means that they routinely interact with conspecifics.

A third area in which the conditions of *A. antipodiana* are unpredictable is in male-male competitions for females. In these interactions it seems that the means by which males compete to gain access to females may require a certain amount of learning, or at least, behavioural plasticity.

The chapters in this thesis are presented in four sections. The first section discusses the social behaviours of *A. antipodiana*, the second discusses male-male competition in *A. antipodiana*, the third discusses the foraging behaviour of *A. antipodiana*, and the fourth discusses the concepts of learning and intelligence and the implication of the above findings. All chapters in this thesis are written as papers and are designed to stand independently.

Section 1, which contains three chapters, examines sociality and its influence on behavioural plasticity. In Chapter 1 I look at the distribution of *A. antipodiana* in the field, and discuss the social grouping of *A. antipodiana*. In Chapter 2 I look at the behaviour by which *A. antipodiana* in groups interact, especially when the animals are kleptoparasitizing the host. The aim of Chapter 2 is to examine whether there is evidence of behavioural plasticity in the social interactions of *A. antipodiana* while foraging. Chapters 1 and 2 reveal interesting characteristics about the way that *A. antipodiana* interact as a group. Consequently, in Chapter 3, I examine sociality in *A. antipodiana*. To do this I first discuss basic concepts of sociality in general, and then use this as a theoretical frame work in which to discuss *A. antipodiana*.

In the second section, which also contains three chapters, I examine behavioural plasticity in male-male competition for females. Chapter 4 describes the basic pattern of male-male competition in *A.antipodiana*, and it also examines the interaction between males who have competed against each other and who are now both trying to mate with the female. (Some of the data in the first part of Chapter 4 was used in my Masters thesis. This chapter is also published in 1991 Behavioural Processes, vol. 23:163-172.) After establishing the general pattern of male-male contests in Chapter 4, I then test conditions that may encourage the development of behavioural plasticity. The first condition, examined in Chapter 5, is the effect of hunger on contests. Hunger is known to have an influence in contests for food. I was interested to see if it could also influence contests for resources apart from food. The second condition that may encourage the development of behavioural plasticity in male contest behaviour, which is analysed in Chapter 6, is past experience. Past experience is known to affect contests between vertebrates (Abbott et al 1985) and even among insects (Otronen 1990). I was interested to see if past experience could affect contests between spiders such as *A.antipodiana*.

In the third section, which contains one chapter, I examine behavioural plasticity in the foraging behaviour of *A.antipodiana*. *A.antipodiana* has a very versatile and complex foraging repertoire. In Chapter 7 I test whether it can modify its behaviour in two of these techniques: feeding with the host, and catching spiderlings.

In the fourth section, which contains 2 chapters, I discuss theoretical aspects of learning intelligence and relate these to *A.antipodiana*. Chapter 8 is a theoretical analysis of 'learning' and 'intelligence'. Both of these terms, and in particular 'intelligence', have been notoriously difficult to define. This has resulted in a lot of on going debate in the literature. In this chapter I discuss the various

ways that people use the words 'intelligence', and suggest a working definition of intelligence designed to facilitate comparisons between species. In Chapter 9 I use the definition of intelligence developed in Chapter 8 in order to examine the types of behavioural plasticity observed in *A.antipodiana*. In this thesis I have assumed that *A.antipodiana* has limited intelligence. In Chapter 9 I test this assumption (using the theoretical framework developed in Chapter 8), and then I examine the means by which *A.antipodiana* has coped with its complex and variable environment.

SECTION I

Sociality and its influence on behavioural plasticity

CHAPTER 1

Group formation

in the kleptoparasitic spider, *Argyrodes antipodiana*.

ABSTRACT

A survey was conducted on the movements of *A. antipodiana* in the field. Results indicate that *A. antipodiana* form groups around the host's webs, but that these groups are not isolated units. Instead, females within a 4 m area regularly move between host webs, re-encountering other females doing likewise.

INTRODUCTION

When it comes to animal groups, what you see is not necessarily what you get: that is, an animal's social unit, which is the individuals with which an animal regularly interacts, may actually be a much smaller group (Schalte and Klingel 1991) or a much larger group (Slooten 1990) than the physical group seen in the field. For example, some mammals may separate into small groups to feed, but their actual social unit (the group of individuals with which they most often interact) is a larger group. For example, Hector's dolphins (Slooten 1990) are often located in small groups, but these small groups regularly merge to form larger groups which appear to be the actual social unit of Hector's dolphins.

Group flexibility is perhaps less common among invertebrates. Among social insects, group flexibility may be inhibited by colony recognition mechanisms. Most colonies have their own distinct badge or label which serves to identify group members and maintain the group cohesion. However,

because these badges also serve to exclude other individuals from the colonies, they inhibit groups combining.

Among most social spiders, fluid groups are also unlikely to develop, but for different reasons. Unlike insects, social spiders do not appear to distinguish between colony mates and strangers. *Stegodyphus mimosarum*, for example, are so tolerant they will even accept a closely related species, *Stegodyphus dumicola*, as part of their colony (Seibt and Wickler 1988). As social spiders have a high tolerance towards conspecifics, they appear to have the potential to divide out into smaller groups and then reform into larger groups, in the manner described for some mammal groups (Slooten 1990). However, it is unlikely that social spiders would develop this form of social flexibility as they have no need to disperse and reform on a daily basis; all their needs are met within the communal web. Thus it is unlikely that many social spider colonies would regularly form sub-groups, as is characteristic of some mammal groups.

One a group living spider between whose aggregations movement may occur is *Argyrodes antipodiana* (O.P. Cambridge). *A. antipodiana* is a small (body length c. 3 mm) kleptoparasitic spider that, in New Zealand, forms small groups (usually of 6-1 adults) around the edge of the orb web of the spider *Eriophora pustulosa* (Walck) from which it steals prey items (Whitehouse 1986, 1988). Although *A. antipodiana* obviously cluster around the host's web, it is unclear whether these groups are temporary aggregations of *A. antipodiana* which continually change their composition as individuals move between host webs, or whether they are a social unit as described above.

To try to ascertain the social organization of *A. antipodiana*, a survey was conducted in an area known to contain *A. antipodiana*. Data were collected on movements between groups, and on the daily movements of individuals within groups. Part of the data was collected in the form of a

time budget to establish the time of day *A.antipodiana* were most likely to travel between web sites, and the home range of spiders resident within a group. The aim was to ascertain whether *A.antipodiana* formed long term groups around host webs or continually moved between host webs. Thus the aim of this study was to decide whether *A.antipodiana* formed social units.

METHODS

Survey

A 14-day survey was conducted in summer (late January 1988) at Te Aroha (North Island, New Zealand) on a small area of residential land (77m x 26m) which was known from previous work (Whitehouse 1988) to be a good collection site for *A.antipodiana*.

The survey was conducted by scouring the study site daily for the presence of *A.antipodiana*. Any *A.antipodiana* that were found were marked with a non-toxic fluorescent paint and returned to the web site from which they were captured. (A "web site" was any place where an adult *A.antipodiana* was found). If a spider was found again after being marked, its colour and location were noted.

Time budget

The three web sites were surveyed every 20 min for 24 h. During each survey the presence, position and activity of each *A.antipodiana* was noted.

Marking spiders

Marking spiders involved anaesthetizing them with CO₂ then applying a small drop of paint to the dorsal and ventral surfaces of their cephalothoraces. Because of the small body size of *A.antipodiana*, it was not feasible to give each individual in the study site an individual code, especially as I decided not to mark the abdomen. The abdomen of

A. antipodiana appears to be made up of a series of silver plates. If paint is put on the abdomen and the animal then feeds, the abdomen is badly constricted at the location of the paint (pers. obs.), undoubtedly causing a lot of stress to the animal. To reduce the stress on the spiders, only the cephalothorax was marked. Because of the subsequent small area available for working and the large number of spiders involved in the survey, individual marking was not attempted. Instead, all individuals from the same web-site were marked with the same colour to ascertain movement between webs.

RESULTS

Survey

At all the web sites (except site 13 where a lone male *A. antipodiana* was found among a few strands of silk), *A. antipodiana* were associated with orb webs. A total of 93 spiders was marked and re-captured over the course of 14 days (Fig 1). Fig 1 shows that many of the *A. antipodiana* caught during the survey had already been marked, and that the number of animals present in the survey area did not fluctuate greatly during the course of the survey, although the ratio of males to females did drop during the period.

Movement between webs

Spiders marked at one web site were readily re-captured at other sites. However, because of the limit on colours, some web sites were labeled with the same colour. If an *A. antipodiana* marked at one web site was found at other web site, it was assumed to have originated from whichever appropriately coloured web site was missing a spider. If the *A. antipodiana* could have originated from two web sites (this happened twice in the surveys for females and four times in the surveys for males) it was assumed that it originated from the closest web site, although the

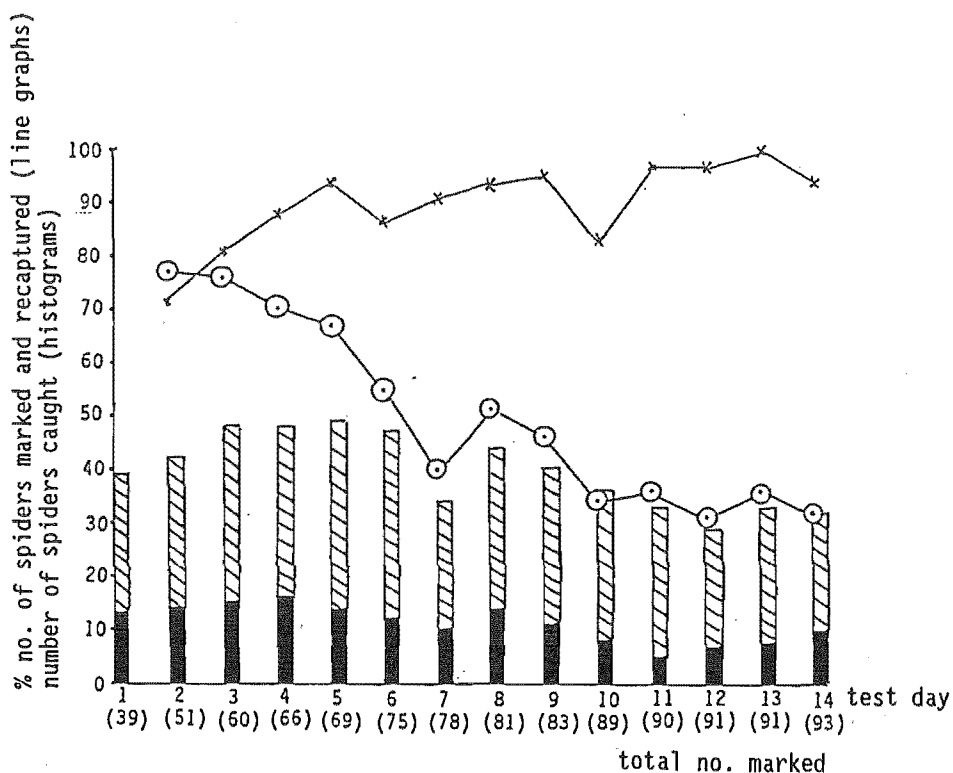


Fig. 1. Spiders caught during the 14-day survey period showing: the percentage of the spiders caught on each day that were marked (line with crosses); the percentage of spiders that had been marked that were re-captured on any particular day (line with circles); the total number of spiders caught on any particular day (histograms: black = male; striped = female); and the total number marked (number in parentheses).

other web site was also noted (Fig. 2 and 3).

Spiders readily moved between webs (Fig. 2 and 3). In particular, there was a lot of movement between groups 9 through 15 and 1 through 3. Interestingly, both spider movement and the web sites themselves, were concentrated along the right border of the survey area. Part of this boarder was a 2 m high corrugated iron fence with bushes in front of it. The rest was a hedge. *A. antipodiana* seems to prefer host webs which have a backdrop of either a thick hedge, a fence, or a bank of a river, and has been seen using these features as a means of traveling between webs (pers. obs.). Thus movement between webs may have been facilitated along this border.

During the survey, males appeared to move greater distances than females. To ascertain if this was indeed the case, the movements of males and females were compared by taking each case where a male or female *A. antipodiana* moved between web sites and recording the shortest possible distance between the web sites. This probably underestimated the distance traveled, because in some instances the shortest distance was across open areas and *A. antipodiana* appear to prefer to move along fences and lines of bushes rather than across open areas. Of the 13 males and 20 females whose movements were recorded, males moved 11.2 m (sd=8.1 m) and females moved 3.6 m (sd=2.4 m). Hence the results from this test indicate that the males moved greater distances than the females (t test: $P < 0.001$).

Time budget

Although it was not difficult to locate *A. antipodiana* with a torch at night (because of the spider's reflecting silver abdomen), many individuals were not located during the night, but were relocated in the early hours of the morning (Fig. 4). Indeed, the *A. antipodiana* at a web site appeared to disperse at night (as much as 1-2 m), making themselves difficult to locate, whereas they grouped closely together during the day.

Fig. 2. The movement of females within the survey area during the survey period. Each arrow indicates the movement of one spider. If a spider was originally found at site 12, and then later at site 10, then this is indicated by an arrow going from site 12 to site 10. Occasionally, there were two sites from which a spider could have originated. When this happened, the most likely site is indicated by the arrow, while the alternative site is indicated in parentheses above the arrow. There are 2 examples of this: the female found at site 11 apparently originated from site 14, but could have originated from site 4; and the female found at site 6 apparently originated at site 4, but could have originated at site 14.

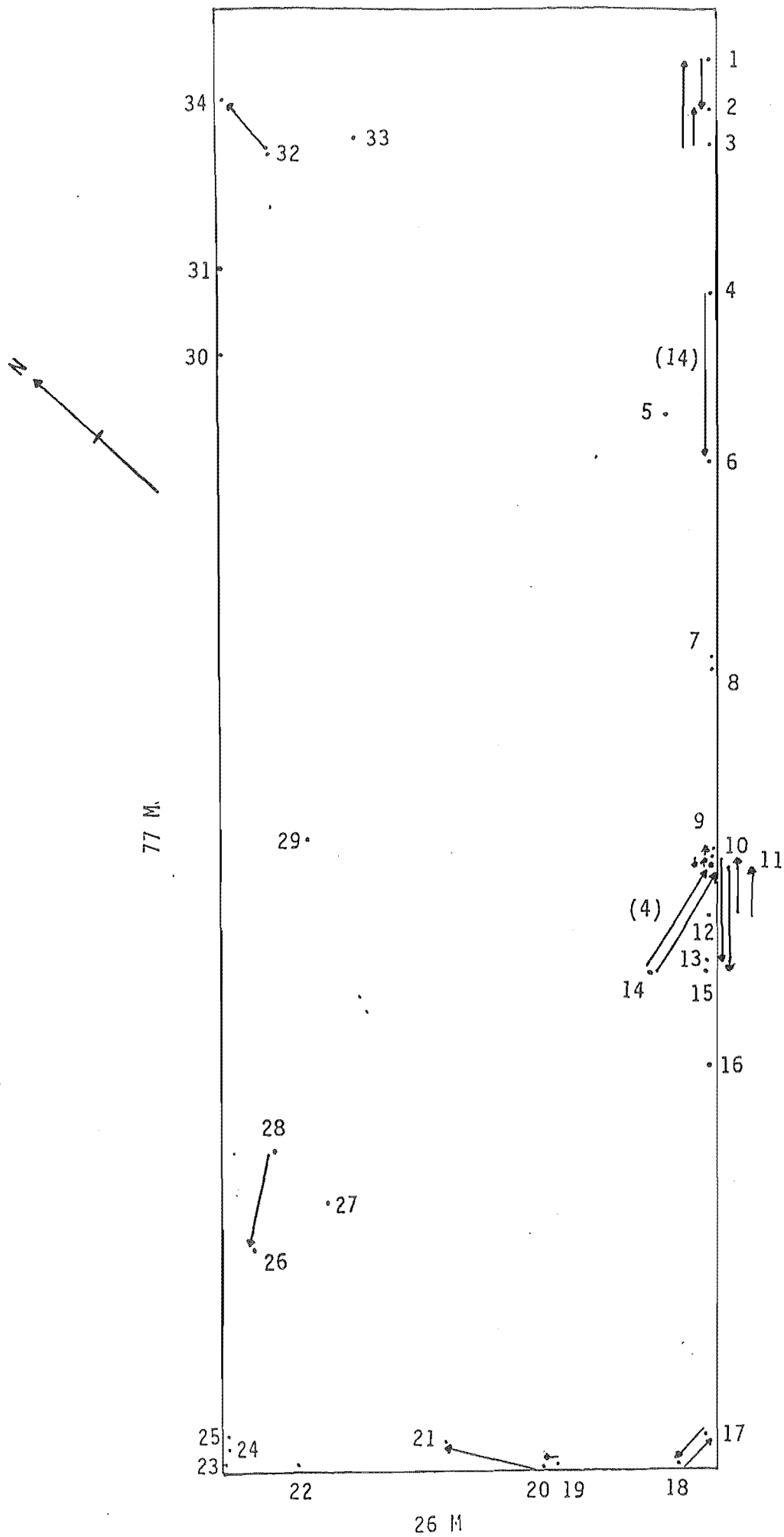


Fig. 3. The movement of males within the survey area during the survey period. To read the figure, see the caption for Fig. 2. Sometimes the same male was recaptured at many different sites. In these cases each site where a male was recaptured is indicated by an arrow head. Consequently, many arrows in this diagram have numerous arrow heads along their length.

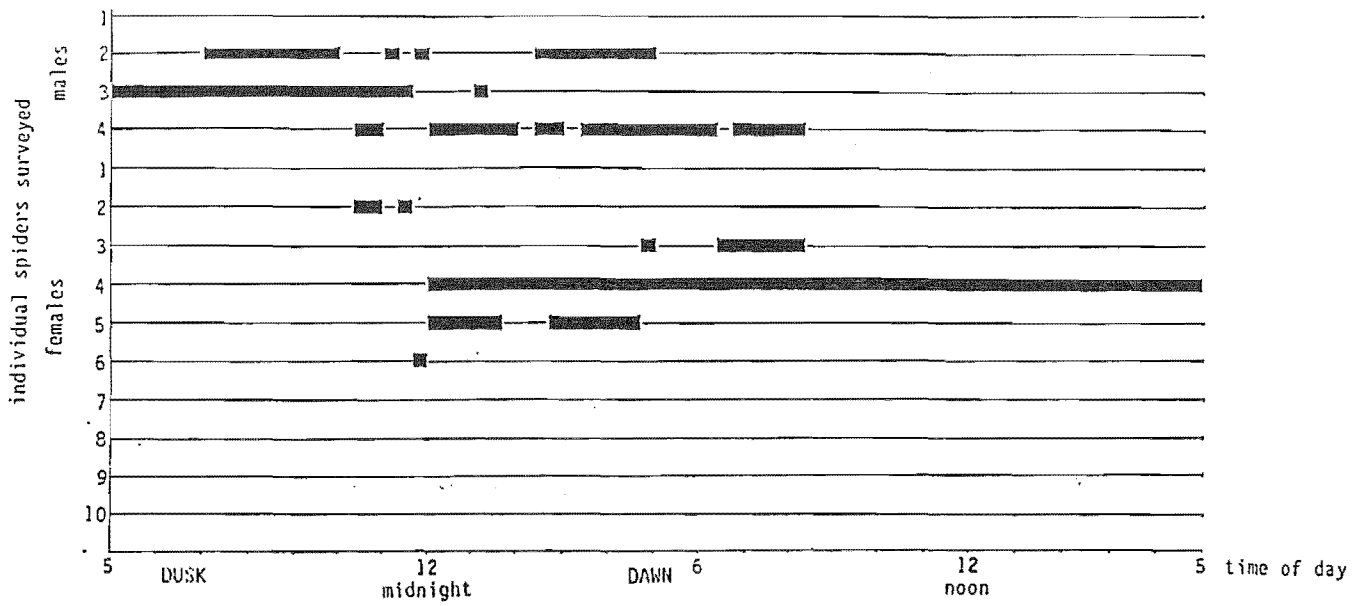


Fig. 4. The presence or absence of four males and ten females at their web sites. Each line represents one spider during the 24 h time budget study. Where the line is thin, the spider was found at the web site, where the line is thick, the spider was missing from the web site. For example, female 4 was present at her web site until midnight, at which time she was missing and she was not relocated at her web site during the rest of the time budget survey.

One female left and one male arrived at web sites during the night (Fig. 4), whereas no movement between webs was seen during the day. This, and the fact that *A. antipodiana* appear to disperse more at night in general, suggests that *A. antipodiana* may be more inclined to travel between web sites at night.

The nocturnal habits of *A. antipodiana* are also reflected in their activities (Fig. 5). *A. antipodiana* spent a lot of time resting during the day, but were alert at night and tended to spend more time moving at night. *A. antipodiana* also mainly fed at night. Only 13 intraspecific interactions were observed, and it was unclear from these whether intraspecific interactions are more prominent diurnally or nocturnally, although it seems that *A. antipodiana* are likely to interact with each other at any time.

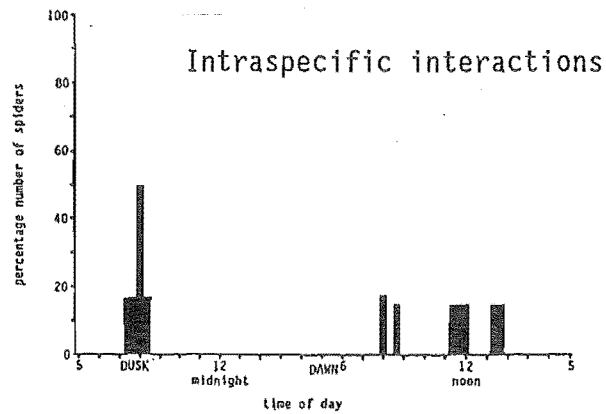
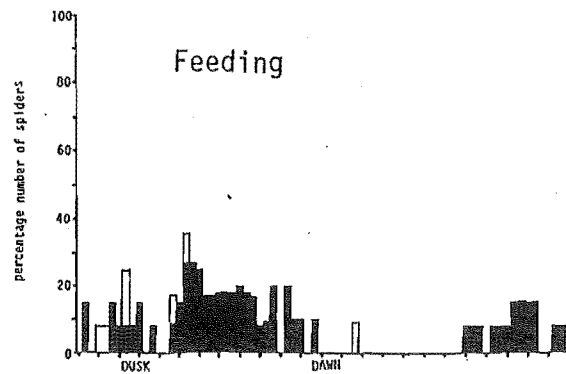
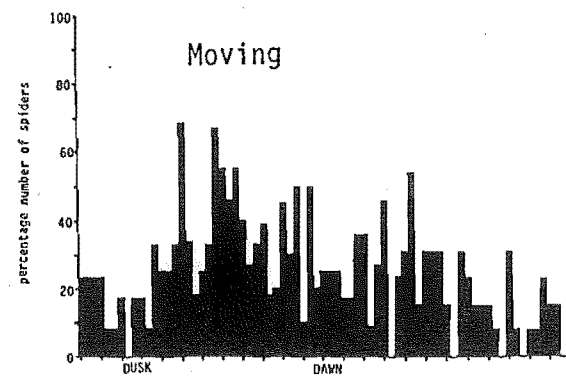
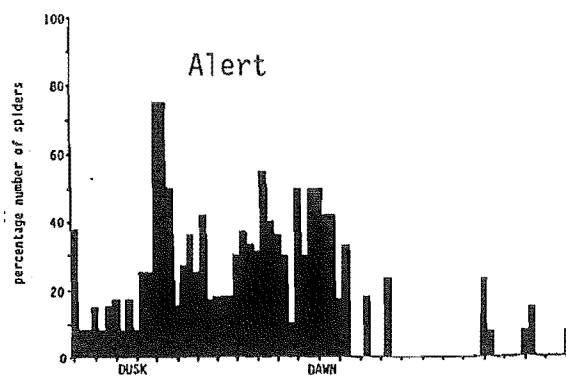
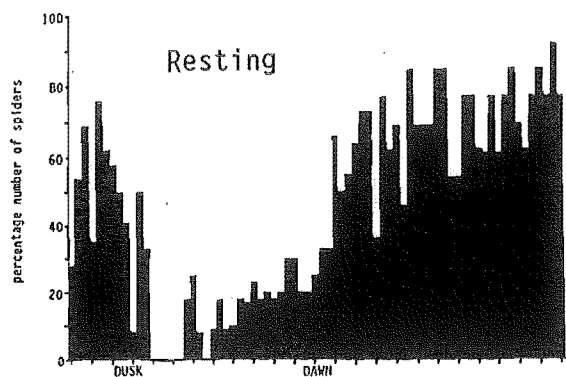
DISCUSSION

The pattern of activity of *A. antipodiana*

A. antipodiana appears to be more active nocturnally than diurnally. This is in contrast to another kleptoparasitic species of *Argyrodes*, *A. elevatus* (Taczanowski). *A. elevatus* appears to prefer to be diurnal, as it is diurnal when it is the only species of *Argyrodes* kleptoparasitizing the web of its host, *Nephila clavipes* (Leach) (Vollrath 1986), although it is nocturnal in the presence of *A. caudatus*. The difference between the preferred period of activity of *A. antipodiana* and *A. elevatus* may reflect the difference in the habits of their hosts. The host of *A. elevatus* is diurnal, whereas the host of *A. antipodiana* is nocturnal.

The host's activities may affect the activities of these *Argyrodes* by triggering their period of activity. That is, *Argyrodes* may simply be active whenever the host is active. The fact that *A. elevatus* becomes nocturnal when kleptoparasitizing in webs shared with *A. caudatus* supports this argument and indicates that the period of activity in these species

Fig. 5. Activity budgets of *A. antipodiana*, revealing the percentage of spiders, at any particular time, which were resting, alert, moving, feeding, or engaged in intraspecific interactions. The number of *A. antipodiana* surveyed during the day ranged from 10 to 13 (as some spiders left their study site during the survey). A spider was resting if it had all its legs drawn in close against its body ('hunched' posture: Whitehouse 1986) or if it had its legs I and II straight out in front of itself so that it resembled a small stick ('extended' posture: Whitehouse 1986). In the graph on feeding the clear bars indicate that *A. antipodiana* was eating silk, while the black bars indicate that it was feeding on prey.



of *Argyrodes* is very flexible and appears to be a form of behavioural plasticity which enables these species of *Argyrodes* to modify their behaviour with respect to that of the host.

The social unit of *A.antipodiana*

The results show that most *A.antipodiana* regularly encounter more individuals than those on the immediate host's web. Males, in particular, tend to move a great deal between webs and probably do not re-encounter individuals with any frequency. This is interesting as it is reminiscent of solitary (rather than social) male spiders which wander in search of females (Bristowe 1958). Males of other social spider species tend to stay on the one communal web (e.g. *Mallos gregalis* (Simon); Jackson 1978b). Female *A.antipodiana*, on the other hand, seemed to be relatively sedentary: although they moved between webs, they tended to stay within a 4 m area. Consequently, females were probably interacting with the same individuals over a period of time.

Thus the social unit of the females was not limited to the females on one host web, but appeared to include all the females on host webs within a few metres of each other. The composition of individuals at any host web varied, but each *A.antipodiana* still appeared to be interacting with individuals from a larger group.

Hence *A.antipodiana* is unusual among group-living spiders in that its social unit apparently consists of flexible subgroups which exploit the host webs within a certain area. Unlike other social spiders whose needs are met on one social, self-built web, *A.antipodiana* may need to move between kleptoparasitized webs frequently in response to changes in these webs, such as lack of prey or desertion by the host (Rypstra 1981). Consequently, the social organisation of *A.antipodiana* is not defined by the boundaries of one web, and appears to be more reminiscent of some social mammal groups than other social spider groups.

CHAPTER 2

Sociality and the dynamics of a foraging group:
the use of conditional strategies by *Argyrodes antipodiana* during
aggressive interactions in competition for food.

ABSTRACT

A. antipodiana kleptoparasitize their host *Eriophora pustulosa* in small groups. Within the groups *A. antipodiana* interact aggressively over food items. This, though, can put *A. antipodiana* in danger of predation from the host which occasionally responds to these aggressive interactions. In response to the conflict between the threat of predation and the problem of intraspecific competition for food, *A. antipodiana* appears to have developed a conditional strategy: *A. antipodiana* tend to interact with conspecifics aggressively in areas of the web complex where predation pressure from the host is reduced, but interact non-aggressively at the hub where predation pressure is great. This strategy appears to be innate. This apparent ability to change interaction intensity in response to its position on the web complex enables *A. antipodiana* to effectively exploit a very risky, but very rich, food source.

INTRODUCTION

Being in a group may be both advantageous and disadvantageous when it comes to obtaining food and avoiding predators. For example, groups may provide protection against predators (Hamilton 1971, Powell 1974) but they may also increase the risk of predation because groups are more visible to predators than solitary animals (Pulliam and Caraco 1984,

Sasvari 1992). Likewise some group-living animals can increase prey consumption because, as a group, they can attack larger prey (Wilson 1975, Nentwig 1985) while other group living animals may suffer from reduced prey consumption because of the cost of increased competition for food (Morgan 1988, Jacob 1991).

Within a group, direct competition between individuals for food may also increase predation risk. When many individuals are competing for the same food item they may be more conspicuous to predators, and their vigilance for predators may also decline. Thus it may be advantageous for animals in high predation risk areas to reduce intraspecific competition. Huntingford (1982) found that populations of sticklebacks from high predation risk areas showed less intraspecific aggression than those from low risk areas. Apparently, this is the result of local adaptation by these populations. However, it might also be advantageous for individual animals to have a conditional strategy by which they reduce intraspecific aggression when in situations of high predation risk. Here, I examine the relationship between intraspecific aggressiveness and predation risk within foraging groups of the kleptoparasitic spider *Argyrodus antipodiana*.

Argyrodus antipodiana (O.P. Cambridge) is a small kleptoparasitic spider which lives in groups around the webs of larger 'host' spiders (Whitehouse 1986, Chapter 1). While living in a group, each *A. antipodiana* exploits both the host and its web. For instance, *A. antipodiana* may glean small insects trapped in the host's web but ignored by the host, it may steal prey caught and wrapped by the host ('foodbundles') or it may even feed with the host.

Feeding with the host appears to have special advantages. *A. antipodiana* is not only parasitizing the host's ability to catch large prey, but probably also it's digestive enzymes. Spiders feed by pumping enzymes into prey, then later ingesting the emulsified viscera. When

A. antipodiana feeds with the host, it almost surely gains access to large vats of "precooked" (predigested) food. However, feeding with the larger host may also be particularly dangerous as *A. antipodiana* can be caught by the host and made part of the host spider's foodbundle.

Additionally, an *A. antipodiana* does not usually kleptoparasitize the host on its own (Whitehouse 1986). Instead, a group of *A. antipodiana* usually forms around a host's web and individuals simultaneously try to approach and feed with the host. It has been observed that when *A. antipodiana* encounters conspecifics on a foodbundle, it aggressively competes for the foodbundle (pers. obs.). However, aggressive interactions between *A. antipodiana* are also known to attract the attention of the host (pers. obs.). Is *A. antipodiana* adapted to balance advantages of aggressively excluding a rival conspecific from food against the danger of the host attacking? In this paper, I examine the hypothesis that *A. antipodiana* has a conditional strategy in which it reduces intraspecific aggressiveness in areas of the 'web complex' where predation risk is higher.

MATERIALS AND METHODS

Background information

A. antipodiana builds a support web within the space web at the top of the orb web of the host, *Eriophora pustulosa* (Walck) (Fig. 1). From the support web, *A. antipodiana* makes sorties on to the host's web either to steal foodbundles (which are then hauled up into the support web) or to feed with the host at the hub. While foraging, *A. antipodiana* extends the support web by connecting threads directly on to the host's web. These threads usually extend right down to the hub. There, direct lines from the hub to the support web provide *A. antipodiana* with a quick escape route should the host detect its presence and a quick re-entry on to the hub once danger has past (for more information on feeding behaviour see

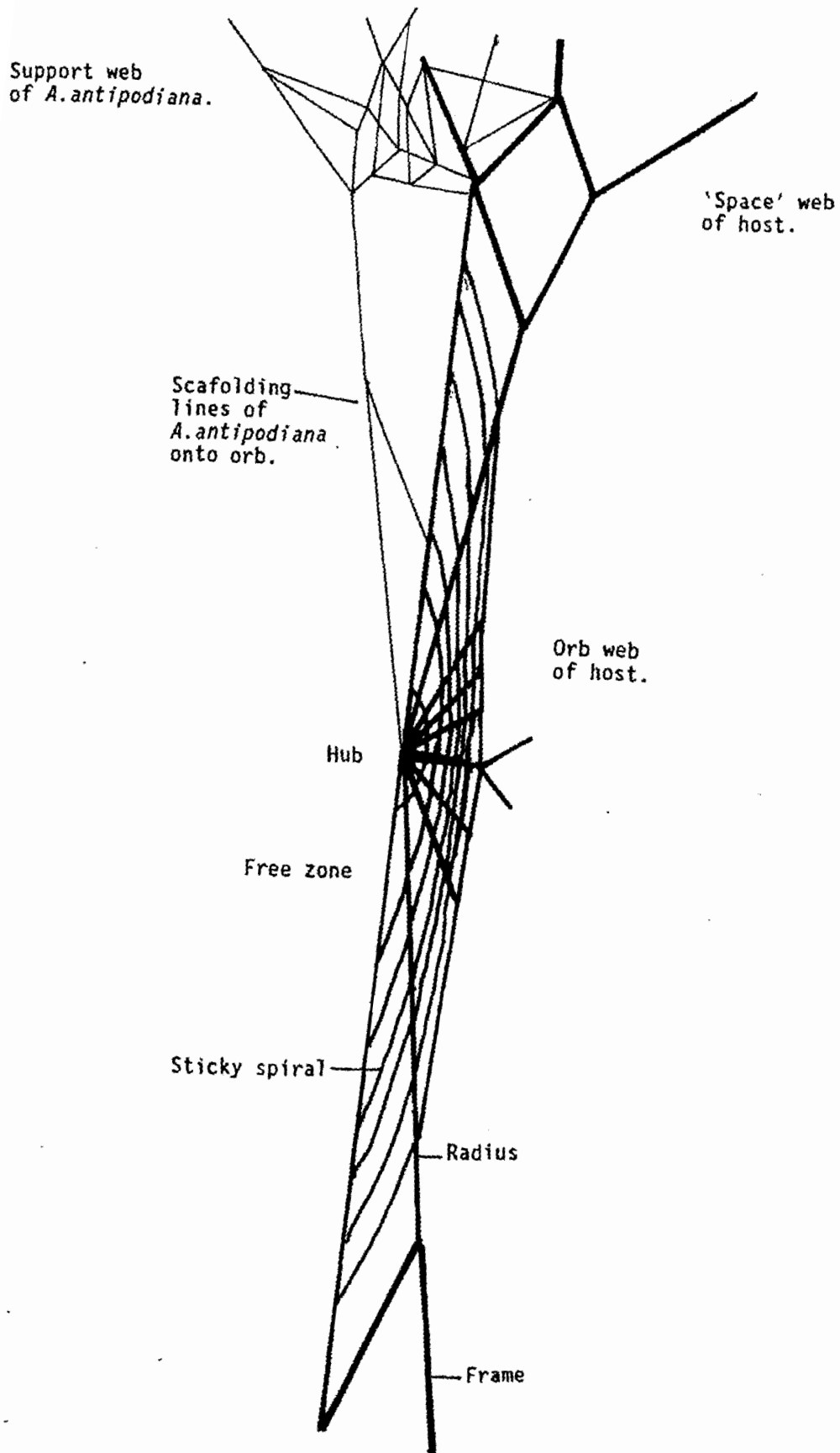


Fig. 1. The web complex, which includes the support web of *A. antipodiana* and the orb web of the host, *E. pustulosa*.

Whitehouse 1986). The host's orb web and *A.antipodiana*'s support web are together called the web complex.

Obtaining inexperienced *A.antipodiana*

Spiderlings were raised from the eggsac exclusively on foodbundles caught by another spider species, *Achaeearanea* sp. (Theridiidae; hereafter referred to as '*Achaeearanea*'). *Achaeearanea* (body length: c. 7mm) was chosen for this purpose because (1) it readily builds very effective webs in confined spaces, (2) these webs were very similar in design to the support webs of *A.antipodiana* and *A.antipodiana* has no difficulty moving on the webs of *Achaeearanea*, and (3) *Achaeearanea* sp. was readily available. To feed *A.antipodiana* on the foodbundles of *Achaeearanea*, *Achaeearanea* was housed in a small (height: 6 cm; diameter: 5 cm) cylindrical container and fed fruitflies (if the *A.antipodiana* to be fed was a juvenile) or a housefly (if the *A.antipodiana* to be fed was an adult). *Achaeearanea* responds to struggling prey in its web by wrapping each prey item in silk, thus creating a 'foodbundle'. After *Achaeearanea* had caught the fruitflies and begun feeding, it was removed from the container while the foodbundles stayed in the web. *A.antipodiana* was then placed in the container where it fed on the foodbundles of *Achaeearanea*.

The *A.antipodiana* raised in this manner had no previous experience of orb webs or of feeding with *E.pustulosa*. Initially, *A.antipodiana* was fed in groups of three, but once juvenile females were 2-3 moults prior to maturity, they were fed, in isolation, on *Achaeearanea* foodbundles until they were used in the tests. Once mature, groups of four females were set up with orb webs as described above. The spiders raised in this manner had no experience, as adults, of other *A.antipodiana*.

Test groups

Eleven groups of four experienced female *A.antipodiana* (i.e. spiders that had grown up on an orb web with conspecifics) and two groups of four inexperienced female *A.antipodiana* were set up in large glass tanks (100x50x60 cm) which contained the host spider and its orb web. All *A.antipodiana* were marked and weighed prior to being set up. All test groups were first tested on day 1, and then once every few days for a period of up to 14 days. Inexperienced *A.antipodiana* were only tested twice (days 1 and 3) to control against the possibility of experience during the test affecting results.

Test procedure

Tests were conducted at room temperature in the early evening when both *A.antipodiana* and the host spider were most active (Chapter 1). To begin the 2-h test, flies stunned by CO₂ were thrown on to the web. As the flies recovered and began struggling, the host spider responded to their movements and caught them. The behaviour of the spiders was recorded throughout the 2-h test period by noting which spiders were interacting, their location on the web complex, and the intensity of the interaction.

The intensity of the interactions of *A.antipodiana* with other *A.antipodiana* was ranked from 0 (very low) to 5 (very high). The criteria I used for 0 and 1 differed when the spiders were at the hub from when they were elsewhere in the web complex. This was because *A.antipodiana* at the hub moved more slowly and 'stealthfully' than it did elsewhere in the web complex (pers. obs.) apparently making it more difficult for *A.antipodiana* to detect a conspecific at the hub. The intensity of the responses were defined as follows:

0. This level identified instances when spiders were close, but were not apparently aware of each other. Thus it was used to help clarify whether *A.antipodiana* was interacting or not. 'Interactions' at this level

were not used in the analysis.

At the hub the response to the conspecific was classified as '0' if the legs of the spiders were less than 1 cm apart but greater than 1 mm apart; while elsewhere on the web complex an interaction was classified as an '0' if the spiders were within 1.5 cm of each other but did not respond to each other's presence.

1. At this level *A. antipodiana* was defined as interacting. It was the point at which *A. antipodiana* appeared to be 'aware' of a conspecific's presence.

At the hub, the response to the conspecific was classified as '1' if the spiders 'rotary probed' (see below) within 5 mm of each other, if they touched each other but made no response, or if their legs were closer than 1 mm. Elsewhere on web complex an interaction was classified as a '1' if one spider 'orientated' (see below) towards the other spider.

2. The response was classified as '2' if at least one spider moved at normal gait away or towards the other spider.

3. The response was classified as '3' if one spider moved quickly (twice normal gait) away from the other, or if one spider broke the silk between the two spiders, thereby effectively separated the two.

4. The response was classified as '4' if one spider 'chased' or 'fast grabbed' at the other (see below).

5. If one spider 'bit' or 'lunged' at the other or the pair 'grappled' (see below) the response was classified as '5'.

Terminology

If two or more *A. antipodiana* were apparently both trying to feed from the same food source and trying to exclude the other from feeding from that food source, they were defined as competing for that food source. Spiders rotary probed with either leg I by moving this leg so that the tip of the tarsus described a circle (see Whitehouse 1986 for a more

detailed description). Spiders oriented towards an object by turning and facing the object in question.

Aggressive behaviours

"Aggression" is a notoriously difficult term to define (see Huntingford and Turner, 1987) although it is usually linked to behaviours which harm or which show intent to do harm towards other individuals. Huntingford and Turner argue that, as the boundaries of the term aggression are hard to determine, it is probably best to view aggression as a particular case of manipulation. This is the view that will be used here. In this study, aggression is defined as a type of manipulation in which one spider tries to harm, or shows intent to do harm towards, a conspecific in order to manipulate the behaviour of that conspecific (i.e., in order to deter the conspecific from approaching the food). Aggressive behaviours, therefore, include: fast grabbing, chasing, biting, lunging, and grappling.

Fast grabbing, which has been described in detail elsewhere (Whitehouse 1991, in prep.), involved one spider pulling with legs I and II very quickly on the dragline of another spider. Chases occurred when one spider moved quickly towards another spider and the second spider moved quickly away. Biting occurred when the chelicerae of *A. antipodiana* connected with another animal. *A. antipodiana* lunged (described in more detail in Whitehouse 1986) when it propelled itself towards its target and simultaneously tried to scoop the target towards its mouthparts with its legs I. A bite occurred if the chelicerae made contact with the opponent at the end of the lunge. Spiders grappled (described in Whitehouse 1991, in prep.) by facing each other and holding their legs I and II stiffly out sideways while shaking their bodies violently.

RESULTS

Interaction intensity of *A.antipodiana* at the hub and elsewhere on the web complex

Of the 44 experienced *A.antipodiana* set up in these experiments, 40 interacted with conspecifics (384 interactions between 50 pairs of spiders) whereas all 8 inexperienced spiders interacted with conspecifics (69 interactions between 12 pairs of spiders). The degree to which pairs of spiders interacted was very variable. Some pairs only interacted once or twice over the course of the experiment, while others interacted repeatedly. Because of this variability, two approaches were taken to analyse contest intensity both at the hub (a potentially dangerous location) and elsewhere on the web complex.

First, I did a detailed analysis of pairs of spiders which interacted more than 10 times. With these pairs, the interaction intensity ranks at the hub were compared with those elsewhere on the web complex using a Mann-Whitney U test.

Second, I took all examples of pairs which interacted both at the hub and away from the hub, calculated the mean interaction intensity in both locations and recorded where it was highest. If *A.antipodiana* interact at the same intensity both at and away from the hub, then there would be no difference in the tendency for either location to have the higher mean interaction intensity.

Experienced *A.antipodiana*.

The first type of analysis was conducted on the data of 8 pairs of experienced *A.antipodiana* (a total of 165 interactions). In 6 of the 8 pairs (Table 1) the spiders interacted less intensely at the hub than away from the hub.

In the second type of analysis on experienced *A.antipodiana*, 19 pairs of *A.antipodiana* interacted at both the hub and away from the hub.

Table 1.

The effect of the location on the intensity of interactions between experienced females (pairs 1 to 8) and inexperienced pairs (pair 9) competing for food. The 'effect of location' indicates whether the spiders interacted differently at the hub than elsewhere on the web. The mode intensity was calculated from the intensity of interactions scale discussed in the text.

Pairs	Mode interaction intensity		n	Effect of location
	Away	At hub		
1	4 (n=9)	1 (n=5)	14	0.005***
2	3 (n=11)	1&2 (n=7)	18	0.007***
3	4 (n=7)	1 (n=6)	13	0.027*
4	2&3 (n=6)	1 (n=9)	15	0.039*
5	3 (n=10)	1 (n=11)	21	0.005***
6	3 (n=33)	1&2 (n=6)	39	0.005***
7	3 (n=24)	3 (n=6)	30	0.097 NS
8	4 (n=14)	1&2 (n=2)	16	0.153 NS
9	4 (n=12)	1 (n=5)	39	0.009**

Of these, one pair scored exactly the same interaction intensity (1) at both the hub and away, 3 pairs had a larger mean interaction intensity at the hub than away, and 15 had a larger mean interaction intensity away from the hub than at the hub (Goodness of fit: $\chi^2=6.72$, $P<0.01$, $n=18$). Thus in this analysis pairs were also more likely to interact with less intensity at the hub than away from the hub.

Inexperienced *A.antipodiana*.

Data from pairs of inexperienced *A.antipodiana* were analysed in the same way as the experienced *A.antipodiana*.

Only one pair of inexperienced spiders interacted more than 10 times at both the hub and elsewhere on the web complex. This pair interacted significantly less intensely at the hub than away from the hub (Table 1).

In the second analysis only three pairs of spiders interacted both at the hub and away from the hub. Of these, one pair interacted more intensely at the hub, and two pairs interacted more intensely away from the hub. Thus these results do not indicate any overall trend.

Behavioural characteristics of competitive interactions

Competition over foodbundles and flies.

The most common form of competition between female *A.antipodiana* was over stolen foodbundles. Of the 45 instances in which *A.antipodiana* was either feeding on a foodbundle or moving a foodbundle, *A.antipodiana* was interrupted by a conspecific in 29 instances. *A.antipodiana* that were interrupting conspecifics appeared to be equally attracted to conspecifics (i.e., they began moving towards conspecifics performing these behaviours) which were either moving foodbundles (16 occasions) or feeding on foodbundles (13 occasions). Nine of the 29 interruptions (31%) were successful in that the original 'owner' was displaced. In response to the presence of another *A.antipodiana*, the 'owner' of the foodbundle responded

by approaching the intruder (7 occasions) or trying to move the foodbundle away from the intruder (6 occasions). On 2 occasions 2 *A.antipodiana* tried to steal the same foodbundle from each other by trying to haul it in opposite directions. In another 4 cases, 2 *A.antipodiana* fed on the same foodbundle, with the owner apparently unaware or ignoring the intruder.

A.antipodiana also competed for flies. There were 10 instances in which *A.antipodiana* tried to subdue houseflies or fruitflies on their own. These movements attracted conspecifics on 3 occasions. On a further 2 occasions, 2 *A.antipodiana* tried to subdue the same fly (by wrapping) simultaneously.

Competition at the hub.

Although *A.antipodiana* was rarely aggressive towards conspecifics at the hub (see below), it would respond to other *A.antipodiana* approaching the host by ascending back into the support web and performing aggressive displays - apparently to stop the other spider approaching the hub. On 7 occasions, an *A.antipodiana* feeding at the hub responded to another in the support web approaching the hub by ascending back into the support web and either fast grabbing, lunging or chasing the newcomer away.

A comparison between experienced and inexperienced *A.antipodiana*.

The manner in which experienced and inexperienced *A.antipodiana* interacted when competing for access to food did not differ, except that the interactions of inexperienced *A.antipodiana* were apparently more likely to alert the host than those of experienced spiders. Forty experienced spiders were involved in 384 conspecific interactions, but the host responded to only 1 of these interactions (by 'shaking' the web); whereas of the 69 interactions between the 8 inexperienced *A.antipodiana*, the host responded to 5 interactions (test of independence: $\chi^2=21.84m$,

P=0.001, n=453).

DISCUSSION

Contest intensity

Results show that foraging *A. antipodiana* were less aggressive (i.e., more tolerant) towards each other when they were at the hub than away. Consequently, *A. antipodiana* appear to use a conditional strategy when competing for food: when *A. antipodiana* is away from the hub, it aggressively excludes conspecifics from food, but when it is feeding with the host at the hub, it tolerates conspecifics.

Additionally, this conditional strategy appears to be innate. The preliminary results from the inexperienced spiders tested here indicate that *A. antipodiana* which have never kleptoparasitized a host's web or, as adults, been in the presence of conspecifics, still reduce aggression when competing for food at the hub. Thus *A. antipodiana* does not appear to need to have experience at interacting with the host, or even of moving on an orb web, to develop this conditional strategy.

Why should *A. antipodiana* be more tolerant at the hub? The answer may be because *A. antipodiana* appears to be exposed to a greater risk of predation from the host at the hub. When *A. antipodiana* feeds with the host at the hub, it is literally under the jaws of the host and can be captured by the host in this position (pers. obs.). Any disturbance that may alert the host to the presence of *A. antipodiana* could easily result in *A. antipodiana* being captured. Elsewhere on the web complex, the risk is not nearly so great, as the host is not in such close proximity. To capture an *A. antipodiana* the host would have to move towards it, thereby alerting *A. antipodiana* which would have plenty of time to swing away. Additionally, host spiders have never been seen to venture into the support web of *A. antipodiana*, suggesting that these are particularly safe structures from the point of view of host-predation.

The danger associated with feeding with the host raises another question. Why does *A. antipodiana* bother to undertake the risky business of feeding with the host at the hub when there are other, safer, methods of feeding? The answer appears to be that feeding with the host is an especially lucrative feeding method. An *A. antipodiana* feeding with the host can double its weight in a couple of minutes (pers. obs.). Whereas an *A. antipodiana* feeding on a housefly may spend forty minutes feeding and only increase its weight minimally. In fact, an *A. antipodiana* feeding with the host appears to visibly expand before one's very eyes!

If a pair of *A. antipodiana* were to be aggressive towards each other while feeding with the host at the hub, the host would be alerted to their presence, and this would not only stop *A. antipodiana* gaining access to this apparently excellent food source, but also expose *A. antipodiana* to predation from the host. Thus the conditional strategy employed by *A. antipodiana* makes it easier for *A. antipodiana* to feed at this apparently rich, but potentially dangerous, food source.

Behavioural plasticity in group interactions

Experienced and inexperienced spiders appeared to differ in the degree to which they alerted the host to their movements. Preliminary results suggest that inexperienced spiders were, in general, more likely to alert the host than experienced spiders. Thus experience of the host and its web apparently enabled *A. antipodiana* to improve its ability to move undetected on the host's web. This has major ramifications. It suggests that *A. antipodiana* is, to a certain degree, able to modify its kleptoparasitic behaviour in response to the behaviour of its host. *A. antipodiana* is known to kleptoparasitize other spiders (e.g. *Nephila edulis*, Elgar 1989) apart from *E. pustulosa*. Consequently, it would be advantageous for *A. antipodiana* to be able to 'fine tune' its behaviour to that the host species it is kleptoparasitizing. Learning is a means by

which an animal can develop solutions to novel, unpredictable problems. It is possible that *A. antipodiana* may use learning to respond to the subtle characteristics of its host in order to 'fine tune' its kleptoparasitic behaviour to that of its host and thus reduce the likelihood of its movements alerting the host. More work is needed to fully examine this possibility.

CHAPTER 3

Sociality and *Argyrodes antipodiana*

ABSTRACT

This chapter examines the sociality of *A. antipodiana*. It does this by first analysing what 'sociality' may actually be. Next it discusses the behaviours which are usually associated with social groups, and then looks at these in relation to social spiders. With this background, the form of sociality expressed by *A. antipodiana* is discussed. I conclude that the development of sociality in *A. antipodiana* appears limited.

INTRODUCTION

In the previous two chapters I have discussed how *A. antipodiana* arranges itself in groups. *A. antipodiana* in New Zealand form small groups around the webs of their larger host spider *Eriophora pustulosa*. Work presented in Chapter 1 showed that the small groups may not be the actual 'social unit' of these spiders, but a sub-section of a larger group. Thus *A. antipodiana* appeared to form groups which spanned a number of host webs. As a consequence of the observations in Chapters 1 and 2, I was interested in examining the form that sociality has taken in these spiders.

The aim of this chapter is to examine sociality in *A. antipodiana*. In order to realize this aim, I will first discuss basic concepts concerning sociality in animals, and then look at the kinds of sociality that have evolved in spiders. This will provide a framework that I will use to then examine sociality in *A. antipodiana*.

DISCUSSION

1 What is a social group?

Many animals are known to live in groups, and the characteristics of these groups vary greatly. For example, some groups are loose aggregations of non-interacting animals around a desirable resource, whereas other groups are very complex, long lasting, cohesive units whose members are constantly interacting. Which of these groups should be called social and which should not is notoriously difficult to decide.

Most of this difficulty arises because sociality can only be defined in behavioural terms even though sociality itself is not a behaviour (Baylis and Halpin 1982). To avoid this problem, perhaps the best way to look at a social group is to see it as having its own set of characteristics which are more than the sum of the characteristics of the individuals which make up the group. Thus a social group, unlike other kinds of groups, appears to have an 'identity' of its own.

For example, a termite colony has an identity of its own in that the colony is capable of feats that the individual termite is not capable of performing (Wilson 1971). If we arbitrarily remove 100 individuals from the colony and immediately put them together, they would not equal a small colony. They would simply be instead, a group of confused termites. These termites as a group would not be capable of doing anything more than what they as individuals are capable of doing.

Likewise, mammal social groups such as hyaenas (Frank 1986) have their own identity. A hyaena social group is arranged so that it works as a cohesive unit, capable of more than what any individual can do. A group of hyaenas collected from many packs would not be capable of functioning as a unit until they had organized themselves socially.

2 Behaviours associated with sociality and social spiders

One reason for defining a social group is to enable the sociality of groups to be analysed. However, defining a social group as a group which has its own 'identity' causes problems as an 'identity' is a difficult thing to determine objectively. Consequently, workers usually resort to emphasizing behaviours commonly associated with 'sociality' when they want to define sociality. This, though, can also cause problems. These behaviours are sometimes mistakenly thought of as defining sociality, even though they are in fact are only a consequence of the social process that is the core of sociality. That is, these behaviours are themselves only indicators of sociality, not a definitive 'test' of whether a group is social or not.

Nevertheless, individuals within social groups do undergo behavioural changes caused by the fact that social groups have their own identity. That is, animals in social groups have a set of behaviours directly related to group living which animals in other types of groups do not have. It is these behaviours that are often used to identify social groups. However, the behaviours which are considered to be important often reflect the type of animal being studied. For example, Kullmann (1972) identified cooperation, interattraction and tolerance as important behavioural characteristics of social spiders. However, many workers also regard recognition of group members as an important characteristic of sociality in general (e.g. Halpin 1980).

In this section I will look at four behavioural characteristics: interattraction, tolerance, cooperation and recognition and discuss these with reference to sociality in spiders.

2.1 Interattraction.

Interattraction occurs when an animal actively 'seeks out' (Phillips 1990) conspecifics and forms groups with these individuals. Most social groups exhibit some form of interattraction. However interattraction is common in animal aggregations not usually considered social, such as woodlice aggregations. Thus interattraction per se may not be a very strong indication of a group's sociality.

2.2 Recognition.

Recognition is regarded as an important characteristic of social groups (Breed and Bekoff 1981). One of the main reasons why recognition appears to be so important to social groups is because it helps in the maintenance of group cohesion (Halpin 1980). For example, a group of a desert isopods (*Hemilepistus reaumator*) stay together because they are able to recognize each other as members of the same group through a signature smell which all members of the group share (Linsenmair 1985). Another example is that honey bees recognize hive and non-hive members by pheromones (Moritz 1988). The pheromones enable them to associate with hive members and avoid bees from other hives.

Group cohesion is also facilitated in animals which recognize each other individually (e.g. the spotted hyaena, *Crocuta crocuta*, Frank 1986). An animal is recognized as a group member and is allowed to associate with the group, or it is recognized as an intruder and either treated with caution or excluded from the group.

Social spiders, however, do not use recognition in order to maintain group cohesion. In social spiders, group cohesion is maintained by both interattraction among spiders and conspecific tolerance. For example, *Stegodyphus mimosarum* are so tolerant that they will even accept members of another species (*Stegodyphus dumicola*) into their webs (Seibt and Wickler 1988). By maintaining group cohesion in this manner, social

spiders compensate for the fact that they do not seem to be able to recognize either individuals or groups.

All forms of recognition would seem to require some degree of learning. That is, in order to recognize an individual, an animal has to be able to remember the characteristics of individuals or groups and then be able to recognize these characteristics at a later date in order to distinguish that individual from others. This same procedure is also necessary in order for an animal to recognize groups. By apparently not recognizing each other individually, or even recognizing groups of individuals, spiders avoid the need to learn the characteristics of individuals or groups. In addition, the means by which *A. antipodiana* appears to do maintain group cohesion (interattraction and tolerance) do not require any form of learning. Consequently, the mechanism of group cohesion in social spiders appears to be more simple than that used by other animals as it does not require learning.

2.3 Cooperation.

Cooperation has often been regarded as a 'key' feature in defining societies. For example, Wilson (1971) defined a society as "a group of individuals that belong to the same species and are organized in a cooperative manner" That is, in his definition Wilson emphasises the role of cooperation. Scott (1989) also emphasised the role of cooperation in defining sociality as is revealed by his statement "cooperation is essential to social organization; otherwise individuals will not stay together".

But even though cooperation may be central to many definitions of sociality, it itself is an exceedingly difficult term to define. In discussions of sociality, it is at best defined only loosely (e.g. Jackson 1978a) but often it is not defined at all (e.g. Wilson 1971, Trivers 1985). The range of behaviours described as cooperative is also great. For

example, cooperative behaviour include behaviours such as co-ordinated hunting where animals adopt different roles in order to catch prey as well as instances where animals simply attack at the same time (e.g. Ward and Enders 1985). As cooperation covers such a large range of behaviours, it is unclear at what point group foraging behaviour becomes 'cooperative'. This problem is well illustrated in social spiders.

2.3.1 'Cooperation' in social spiders: the role of the web.

The problem of distinguishing between 'cooperative' behaviour and non-cooperative, concurrent foraging behaviour is well illustrated by social spiders. In some social spider species, such as *Mallos gregalis*, many hundreds of individuals occupy the same web, and capture and feed side-by-side on the same prey item (Jackson 1979b). The foraging behaviour of this species appears to be cooperative because these animals appear to be working together to bring down prey (Ward and Enders 1985); but are these animals really working together, or are they simply doing what they would do if they were on their own? Jackson (1979a) argues that the foraging behaviour of *Mallos gregalis*, does not appear to be a co-ordinated attack because it is really the sticky web which catches the prey, not the spiders. The spiders simply come down to feed.

Thus the social activity of the spiders appears to be simply to feed together: they do not need to cooperate to bring down the prey, and they are not behaving any differently from how they would behave if they were foraging on their own. Thus they do not appear to be performing cooperative attacks because they do not appear really to 'attack' prey. Instead, they appear to be very tolerant of conspecifics and this may be the primary factor accounting for feeding in groups.

2.3.2 'Cooperation' in social spiders: every woman for herself.

This argument can be extended to social spiders which do need to act together to capture the prey (Phillips 1990). The argument is as follows: In order to subdue a large prey, more than one spider is often needed in the attack on the victim. Previous workers have concluded that, as one spider can not capture the prey on its own, attacking as a group in this manner is cooperative. However, in her work with *Stegodyphus sarasinorum*, Phillips points out that although the spiders are attacking as a group, the spiders are not apparently behaving any differently from how they would behave if they were catching a smaller insect on their own. Therefore, it may be that prey capture in these spiders is not cooperative but simply a case of each spider responding individually to a struggling prey.

2.3.3 Evidence of cooperation in spiders.

There is, though, evidence that some spiders do act cooperatively. For example, some spiders are reported to recruit others to help capture a struggling prey (Bradoo 1980). However, these reports have been difficult to confirm (Ward and Enders 1985). There are also reports that spiders feeding in a group upon a large prey do not pump as much enzyme into the prey as those feeding on their own (Ward and Enders 1985). Although this last example does imply that the spiders are behaving differently when feeding as a group than feeding on their own, the behaviour does not appear to be cooperative, but exploitative.

Consequently, it seems unlikely that spiders are actually 'cooperative' in any especially interesting way. However, because of their tolerance towards conspecifics, social spiders may often have group behaviours that appear to be examples of 'cooperation'.

2.4 Tolerance.

Tolerance seems to be the key attribute for understanding spider sociality. For example, solitary spiders are extremely intolerant of conspecifics, whereas the most 'advanced' type of social spider (Uetz 1988) are exceedingly tolerant. These exceedingly tolerant spiders, called 'communal non-territorial' (sensu. Jackson 1978a), tolerate conspecifics in close proximity at all stages of their lifecycle, and during all forms of activity (such as feeding or resting).

Other forms of spider sociality appear to vary in the amount of tolerance that the spiders have towards conspecifics. However, the tolerance of spiders towards conspecifics does not vary linearly along a continuum from solitary to communal non-territorial. Spider tolerance of conspecifics can vary in a number of different ways. For example, the actual distance tolerated between conspecifics can vary, tolerance can change in response to a change in activity (e.g. resting to feeding) and the amount of tolerance can change during the lifecycle of the spider.

2.4.1 Distance tolerated.

Firstly, the actual distance tolerated between conspecifics can vary, in that some spiders will allow others very close, while others will tolerate conspecifics only at a web's length. This form of tolerance variation has been used in a classification system of spider sociality. Jackson (1978a) proposed classifying social spiders into 'communal-territorial' species, where webs are interconnected but individually occupied and defended, and 'communal non-territorial' species, where spiders all occupy one simple web and there is little aggression. The difference between these two groups is their degree of tolerance towards conspecifics. One group (communal territorial) will only tolerate conspecifics up to the edge of the web, while social spiders of the other type (communal non-territorial) do not recognize territorial

boundaries: they are completely tolerant of conspecifics. This method of classification is useful. However it only looks at one way in which spider sociality can vary as it does not accommodate the other ways in which tolerance can vary.

2.4.2 Tolerance in relation to behavioural activity.

Tolerance may also vary depending on the behavioural activity. For example, a spider like *Araneus sermoniferus* has a communal resting area, but separate prey-capture webs (Kullmann 1968). Thus they are much more tolerant of conspecifics while resting than while feeding.

2.4.3 Tolerance and the life cycle of the spider.

Tolerance may also vary during the lifecycle of the spider. Some species, such as *Theriodion pictum*, are very tolerant of conspecifics when they are juveniles, but become progressively less tolerant as they get older (Ruttan 1990).

2.4.4 Conclusions about tolerance and sociality.

Accepting that different degrees of tolerance are the major behavioural differences between different forms of spider sociality has a number of consequences. Firstly, as tolerance can vary in a number of different ways it implies that sociality can not be expressed along a continuum, indicating that identifying different 'levels' of sociality is difficult. There have been numerous attempts to try to categorize social behaviour in spiders (Shear 1970, Kullmann 1972, Jackson 1978a). However, most of these have been attempts to base the categorization of 'degree' or 'level' of sociality attained by the species. Thus, there seems to have been an assumption that spider sociality can be viewed as forming a continuum. The view of sociality presented here emphasizes that tolerance is the main factor, but that tolerance can vary in a least three important

ways. Therefore, spider sociality may fall anywhere within a 'three-dimensional area'.

2.5 Conclusions about spider sociality.

In this section I have argued that the most important behavioural difference between different types of social spiders is differences in level of tolerance. Perhaps a classification system based on the type of tolerance a social spider exhibits would be more useful for spiders than a classification system which aims to distinguish different 'levels' of sociality. A classification system based on tolerance would perhaps allow a more homogeneous grouping of animals and consequently a more useful means of viewing spider sociality.

3 The sociality of *Argyrodes antipodiana*

As part of the work for Chapter 2, I observed 384 interactions between 44 *A. antipodiana* living in 11 groups of 4 spiders each, with each group associated with a different host's web. From my observations, it appeared that *A. antipodiana*, like other spiders, showed no evidence of cooperation or recognition. However, *A. antipodiana* did show some degree of tolerance. *A. antipodiana* were tolerant of each other while resting (i.e. they would rest close to each other on the support web). However, *A. antipodiana* were intolerant of each other while foraging. For example, *A. antipodiana* actively defended any food items they encountered and regularly chased each other away from food sources. Any food sharing away from the hub appeared to be unintentional, in that one spider may have managed to start feeding on another's foodbundle while the second spider was unaware of its presence. There was an exception to this, and that was when *A. antipodiana* were feeding at the hub with the host (Chapter 2). Here, the threat of predation appeared to override the spider's normal intolerance of conspecifics while feeding, allowing *A. antipodiana* to feed

side by side.

Hence the degree to which *A.antipodiana* would tolerate conspecifics appeared to be related to the behavioural activity being undertaken. *A.antipodiana* tolerated each other when resting, and when feeding at the hub, but were intolerant when foraging.

Therefore it appeared that *A.antipodiana* were not particularly social. The manner in which they interacted with other individuals seemed to be largely determined by their current behavioural activity (e.g. whether they were foraging, or whether they were on the hub or not) rather than in response to the individuals around them. *A.antipodiana* tolerated the presence of conspecifics on the same web, and possibly used them as much as possible, but showed no evidence of cooperating or developing recognition. Tolerance, cooperation and recognition and interattraction can only be used as indicators, rather than tests, of sociality. Nevertheless, the limited use of these behaviours by *A.antipodiana*, and the lack of evidence of groups of *A.antipodiana* having their own identity, suggest that the development of sociality in *A.antipodiana* is, perhaps, limited.

SECTION II

Behavioural plasticity in male-male competitions

CHAPTER 4

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To mate or fight? Male–male competition and alternative mating strategies in *Argyrodus antipodiana* (Theridiidae, Araneae)

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Abstract

Argyrodus antipodiana is a kleptoparasitic spider that builds its own web around the webs of other, larger host species. Males are more prone to have contests on webs of conspecific females than on webs of conspecific males. Males are also more likely to escalate interactions when on the females' webs than on males' webs, consistent with predictions from game theory models. Yet, in nearly half the tests, males on females' webs did not escalate. Instead of just being "sampling error", these failures to escalate may reflect the contest losers' abilities to gain copulations by "sneaking", an alternative mating tactic which enables males to obtain access to a female, not by fighting, but by exploiting the dominant male's dilemma of whether to mate or fight.

Key words: Sexual competition; Alternative mating strategy; *Argyrodus antipodiana*; Spider; Game theory

Introduction

Often animals compete for important resources by performing displays rather than fighting. Game theory arguments have been used to show how such behaviour can be evolutionarily stable (e.g. Maynard Smith 1974, Parker 1974, Maynard Smith and Riechert 1984). Some predictions extrapolated from game theory models are that

individuals will (1) escalate contests more when the resource at stake is more valuable, (2) balance the costs of the interaction against the benefits of winning the resource, (3) use displays to assess each other's resource holding potential (RHP), (4) display with uniform intensity, regardless of how much longer they are actually willing to fight, and (5) use initial asymmetries between contestants (e.g. prior ownership or size) to settle conflicts (but see Grafen 1987). These and other predictions are generally upheld, but there often are individuals that fail to behave as predicted (eg Austad 1983, Riechert 1986, Turner and Huntingford 1986, Eckert and Weatherhead 1987). One explanation for this is that these individuals have alternative ways to gain access to the contested resource without resorting to direct, aggressive confrontation.

Male-male competition for a limited resource (females) was examined using *Argyrodes antipodiana*, a spider from New Zealand. *A. antipodiana*, like other species in this genus (Vollrath 1976, 1979), is a kleptoparasite of larger spiders (Whitehouse 1986). Also, unlike most spiders, it lives in groups. These groups generally consist of about four individuals living in an irregular space web attached to the orb web of the host. Individual *A. antipodiana* (herein referred to simply as *Argyrodes*) move about slowly and stealthily to glean trapped insects off the host's web, to steal wrapped-up food bundles from the host, and to feed simultaneously alongside the host on the same prey item.

Argyrodes males can distinguish between the silk of male and female conspecifics (Whitehouse, submitted). Thus the presence of females' silk in a web indicates to a male the potential presence of a mate (an especially valuable resource). For males, then, webs vary in resource value, enabling the outcomes of contests between males on different types of webs to be used to test predictions derived from game theory models. In a number of studies, however, animals that lose contests for access to females, or avoid contests altogether, gain access to females by other means (e.g. Ryan and Causey 1989, Kodric-Brown 1986). Perhaps this is true also of *Argyrodes* males.

If two males of any given species simultaneously try to court and mate with the same female, each male may face a dilemma as to whether to respond to the competitor or to the female. To solve this problem, at least four different responses by males might be predicted. Firstly, males might avoid confrontations with their opponents and concentrate on courting and mating with the female either by totally ignoring the opponent or by actively avoiding the opponent. Alternatively, males might stop courting the female and concentrate on chasing the opponent away or disrupting the opponent's copulation attempts. Other work has shown that males that "sneak" copulations tend to avoid their opponents (Crespi 1986) most of the time although they may try to disrupt their opponent's copulation attempts (Kodric-Brown 1986). Dominant males often chase other males away from females (Peschke 1987, Crespi 1986) and disrupt other males' copulation attempts (Cox and Le Boeuf 1977).

In this paper, three hypotheses about male-male interactions of *Argyrodes* are investigated: males are more inclined to have contests when on a female's web than when on a male's web; contests escalate to higher levels on a female's than on a male's web; and "losers" of aggressive contests are able to use alternative tactics to mate with the female. The responses of the males to each other and to the female will also be examined.

Methods

Maintenance

All spiders were collected from Te Aroha (North Island, New Zealand) and were maintained according to general procedures for spider studies described elsewhere (Jackson and Hallas 1986), in a room with controlled photoperiod (12:12, L:D) and temperature (20–25°C). Observations took place during daylight hours.

Tests for male–male contests

In each test, two males were introduced simultaneously to a recently (5–20 min) vacated web of either a conspecific male or a conspecific female. Each pair of males was tested on a male's and on a female's web on consecutive days (order random). The males were left on the web for a 20-min test period and were observed continuously. Twelve pairs of males were weighed (using a Cahn 21 electrobalance) before testing. Although each individual male was used more than once, a given pairing of two males was used for only one pair of tests. Results were analyzed using the McNemar tests for significance of changes with Yates' Correction (Sokal and Rohlf 1981).

Tests for mating tactics

Two males were placed on the web of a female, with the female present, and the ensuing interactions observed until the trio became quiescent or 5 h had elapsed. If the spiders failed to interact within the first 30 min, the test was aborted. Although individual males were sometimes used in more than one test, a given pairing of two males was used only once.

Interactions were video taped for later analysis. Information was gathered to establish the following: which male obtained the most copulations and which male copulated for the longest total time. If both males copulated, the reaction of each male to the other was examined.

Results

Male–male contests

Terminology

Animals "escalated" an interaction when they progressively switched to behaviours of greater "cost" (Fig. 1). Cost of a behaviour was estimated, not measured, based on judgment of the degree of danger to which the spider probably exposed itself when performing the behaviour. For instance, by shuddering, a spider apparently alerts its rival and thereby becomes more vulnerable to attack by the rival. Touching is ranked

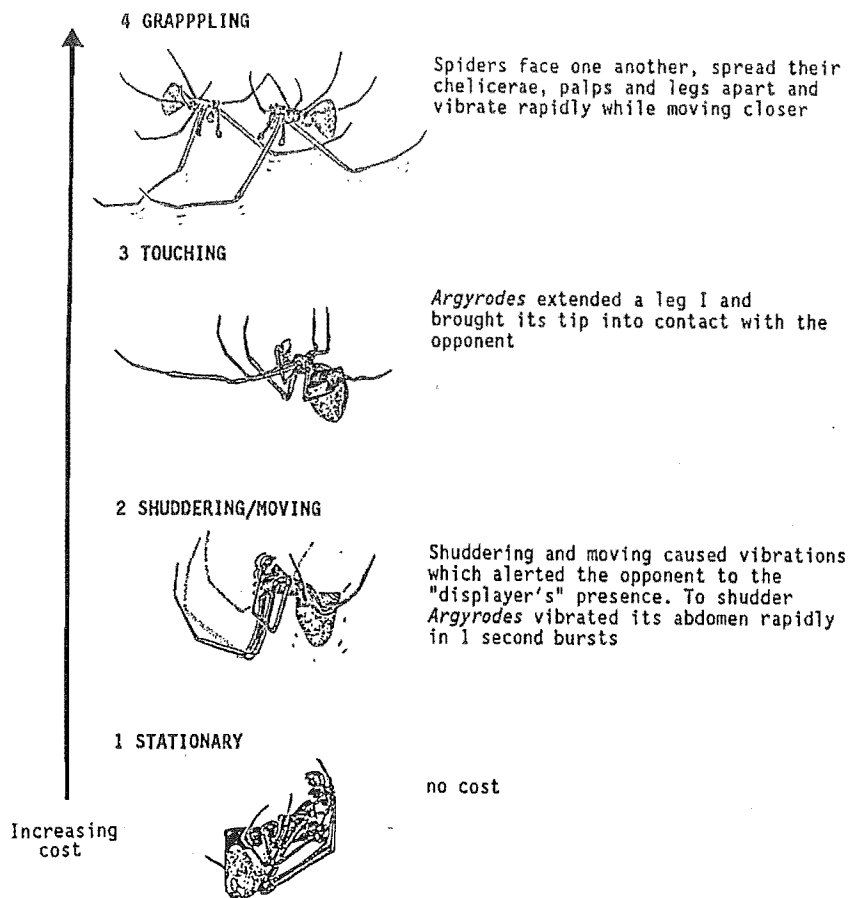


Fig. 1. Diagrammatic representation of escalation in fights between male *Argyrodes antipodiana*. The fight escalated when it moved to the next level in "cost" which was estimated arbitrarily on the amount of probable danger the display exposed the actor to.

higher than shuddering because touching is possible only when the rival is close and, at close range, the rival can readily attack. In fact, *Argyrodes*, on rare occasions have been seen to lunge suddenly at other *Argyrodes* from close range (unpubl. data). Grappling, which can last over 2 min, is ranked still higher because this behaviour takes place with spiders almost touching each other and apparently in positions from which they could readily bite each other. Grappling spiders move closer and closer together, then, if neither spider breaks off the interaction, the spiders lock chelicerae together. Only a shift in position of chelicerae would seem necessary to inflict serious injury or death on a rival.

A spider "avoided" another when it moved at its normal speed away from its rival, while "chasing" occurred when one spider quickly moved towards its rival and its rival quickly moved away, excluding interactions in which one male was initially copulating.

In a "contest", the "winner" was a spider that consistently moved towards the other spider (the "loser") which, in turn, consistently moved away. There were two types of contests depending on whether or not a spider fast grabbed.

TABLE 1

Level of escalation reached by pairs of males on male and female webs.

Level of escalation	1	2	3	4
male web	3	17	2	0 n = 22
female web	4	6	5	7 n = 22

To "fast grab", one spider (always the winner) pulled rapidly with his front legs on the dragline of the loser, as if he was trying to haul in the other spider. Once a spider had fast grabbed at its opponent, he was very rarely (4 cases out of 151 chases) chased again by his opponent. Contests in which the winner fast grabbed are called type 1.

In tests where spiders did not fast grab (type 2), the two spiders tended to take turns chasing each other. In these tests, the "winner" was the spider that predominantly (more than c 80% of the time) chased the other male (the loser). If spiders chased each other equally, no winner or loser was designated.

It needs to be emphasized that fast grabbing and chasing were not simply steps in escalation sequences. Instead, they could occur after any of the other behaviours (Fig. 1).

Findings

Out of 22 test pairs, males fast grabbed (i.e. had type 1 contests) in only one interaction on males' webs but fast grabbed in 16 interactions on females' webs, indicating that males are more inclined to contest a female's web than a male's web ($\chi^2 = 11.53$, $P < 0.001$).

Male-male interactions tended to escalate to higher levels on females' webs than on males' webs (Wilcoxon's signed rank test, $P < 0.05$, $n = 22$ test pairs). Nevertheless, in nearly half the tests (10), males did not escalate beyond level 2 on females' webs (Table 1). In these instances, though, "winners" and "losers" were still established in type 2 contests.

In the 12 tests with weighed males on females' webs, larger spiders usually won the fights (8 out of 12 tests). There was no evidence, however that escalation correlated with size difference (multiple regression: $r = 0.004$, NS).

Mating tactics

Terminology

"Copulation" is defined as the period during which the male's palpal organ was engaged on the female's epigynum. Spiders are "courting" if they are performing displays specifically associated with mating as defined in Whitehouse (in prep.). One male "disrupted" another male's copulation by moving towards, displaying towards, or touching the copulating pair, resulting in the pair separating.

To "drum", a male extended his straightened legs I anteriorly and moved them up and down in alternating phase (i.e., when one leg is maximally dorsal, the other is maximally ventral), articulating at the bases of the legs (the coxa-trochanter joints) so rapidly that the two moving legs appeared as a blur.

TABLE 2

Interactions between individuals within tests.

* both copulations took place with the second male before the males fought (the female showed no interest in copulating after the fight).

Test	Total period of activity	Total number of interactions	Number of copulations	Number of male-male interactions	Number of male-female interactions (excluding copulations)
1	2 h	18	2 *	2	14
2	5 h	227	50	103	74
3	4 h	175	49	49	77
4	3:20 h	130	45	28	57
5	2:40 h	186	45	67	74

Findings

Individuals interacted in 10 tests and winners were established in each. Fights escalated to grappling in 8 of these tests. Females were receptive, though, in only 7 of the 10 tests, and in 2 tests the female copulated only once (in one case for 3 min, in the other for 38 min). Thus, only 5 tests were available for full analysis.

Gaining copulations

Once interaction with the female began, the winner and loser of the preceding fight were called the "first" and "second" male, respectively. There were four tests in which the female copulated more than once after the males' contest. In each of these tests, both the first and second male managed to copulate with the female (Table 2). The usual sequence of events was that the males fought, apparently for access to the female, and the winner then mated with the female. However, in test 1, the second

TABLE 3

Copulation behaviour. The numbers in the parentheses are the percentages of the copulations performed by the male that were disrupted.

Test	Number of copulations		Time spent copulating		Number of copulations disrupted	
	Male I	Male II	Male I	Male II	Male I	Male II
2	42	8	24:16 min	13:47 min	20 (48%)	5 (63%)
3	42	7	25:49 min	6:56 min	9 (21%)	3 (43%)
4	42	3	27:14 min	4:05 min	10 (24%)	2 (67%)
5	36	9	18:21 min	16:15 min	21 (58%)	8 (89%)

male managed to copulate with the female before the males fought, and the female refused to copulate after the fight. Thus test 1 could not be used for further analysis.

In all tests, the spiders were active for 2 to 5 hours, with the individuals in most tests interacting over 100 times (Table 2). The first male always interacted more with the female, and obtained many more copulations than the second male (Table 3), although in test 5 the second male spent almost as much time mating as the first male.

Chasing and avoiding

There was a total of 249 male–male interactions. The first male chased the second male in 147 of these, whereas the second male chased the first in only 4. The second male avoided the first male 89 times, but the first male never avoided the second male. Thus the first male predominantly chased the second male whereas the second male predominantly avoided the first. However, the second male often approached and courted the female while the first male was away from the female and actively moving over the web. For example, in 13 of the 147 instances in which the first male chased the second, the second male was able to return to the female while the first male continued moving away from the female, apparently still trying to chase the second male. Males also interacted by courting each other 9 times (i.e., they performed the same displays that are normally performed only in male–female interactions).

Disruptions

Males often disrupted each other's copulations (Table 3). In all tests, however, there were more disruptions of the second than of the first male's copulations. The second male disrupted the first male's copulations primarily by courting (16 times), touching (16 times), drumming (9 times), moving towards (8 times), or shuddering (5 times). The first male disrupted the second male primarily by touching (5 times) courting (4 times), trying to mate (4 times), or moving towards (2 times). Thus the first male usually disrupted the second's copulations either by directly trying to mate with the female or by touching the pair; he did not drum or shudder to disrupt copulations, as was often characteristic of the disruption attempts by the second male. Disruptions were directed at the male, the female or both.

Simultaneous courtships

Males courted simultaneously on 25 occasions. Nine of these courtships ended with the female being aggressive towards one or both males and 2 simultaneous courtships ended when one male chased the other. Females did not appear actively to choose one male over the other in any of the tests with simultaneous courtship by 2 males.

Discussion

Males were more likely to fight when on females' webs, and contests on females' webs escalated to higher levels than those on males' webs. Yet, in half the contests on females' webs, there was no escalation, despite the evident importance to the males of the resource being contested. Lack of escalation does not seem to be attributable simply to differences in size, as this would have resulted in a negative correlation

between size difference and level of escalation, as shown by Wells (1988). Such a trend was not evident in the 12 tests using males of known weight.

To understand why males did not escalate, it may be important to ask whether males have alternative ways of gaining access to females. It is helpful to envisage competition between males for access to females as being divided into two contests. In the first, a ritualized fight establishes a winner and a loser. In the second, both the loser (who stays in the web) and the winner try to mate with the female.

In the second contest, the first male (i.e. the winner of the fight in the first contest) obtained more copulations and copulated for longer. He actively chased the second male away from the female, and disrupted the second male's copulation attempts. The second male, in contrast, tended to obtain fewer copulations than the first, avoided the first male by moving away from him, and very rarely chased the first male, but did disrupt the first male's copulations. It appears, therefore, that in these encounters, the first male was "dominant" while the second male gained copulations by sneaking.

However, the picture is not as straightforward as this because the first male tolerated the second when both courted the female simultaneously, and the second male disrupted the first male's copulation attempts.

To understand these behaviours, it is necessary to consider the options available to a male when another male is courting the same female. A male might avoid or ignore his opponent and just try to mate with the female, or he might chase or disrupt his opponent. It was usually the first male that chased the second male away rather than vice versa. Chasing an opponent away, however, had disadvantages for the first male because, to do so, he had to terminate his own copulation attempts and the second male always returned. As an alternative, the first male occasionally ignored its opponent and continued to court and copulate with the female.

The first male appears to be faced with a dilemma of whether to mate or chase and this may have helped the second male obtain copulations. To mate, the first male must ignore the second male, enabling the second male to approach the female. To attempt to chase the second male away, the first male has to leave the female, providing the second male with an opportunity of finding the female, courting and copulating with her.

Although the second male usually avoided the first male, he did sometimes actively disrupt the first male's copulations. The second male did this mainly by performing courtship displays: in these instances, the second male may have been ignoring the first male and simply attempting to mate with the female. Nevertheless, the second male did sometimes seem to disrupt the first male's copulations deliberately by drumming at the pair. *Argyrodus* males are very sensitive to distraction while mating and readily separate from the female when disturbed, but the process of untangling itself from copulating with female apparently entails a delay in the copulating male's attack on the disrupter. Because of this, second males appear to be able to disrupt the first male's copulation attempts with relative impunity.

Does the second male's tactic of sneaking copulations seriously undermine the first male's success? Does the option of sneaking undermine the importance of winning the initial fight?

There are a number of factors that probably affect the second male's prospects of fertilizing eggs. First, the second male did not spend as much time mating as the first, suggesting that second males tend not to transfer as much sperm as first males.

However, it is not clear when, during the c 5 hours of courtship and copulation, the majority of sperm is actually transferred. Some behaviours, classified as "copulations", probably are actually courtship or even plug depositing behaviours resulting in no sperm transfer (Whitehouse submitted). Second, Austad (1984) suggested that spiders with conduit spermathecae are morphologically predisposed to use sperm in the order in which it is deposited. *Argyrodes* has conduit spermathecae, suggesting that the first male tends to have an advantage as he usually mates with the female immediately after the fight and before his competitor can sneak copulations. However, the first male to mate is unlikely to fertilize all of a female's eggs. It is known that partial displacement of sperm by the second male, or a mixing of sperm from the two males, occurs in some spiders with conduit spermathecae (Jackson 1980). Sperm usage patterns by *Argyrodes* have not been studied, but it seems probable that sneaky copulations are an effective alternative mating tactic and the availability of this tactic to *Argyrodes* reduces the importance of winning fights.

CHAPTER 5

The effect of feeding on the ability of males of the spider
Argyrodes antipodiana to compete for access to females.

ABSTRACT

Hunger is known to affect aggressiveness between animals competing for food (e.g. Bishop et al 1978, Barnard and Brown 1983). Experiments were conducted to see if hunger could influence the general aggressiveness of an animal to the extent that it would be inclined to compete more rigorously for other resources apart from food. To do this, tests were conducted on naive adult male *A. antipodiana* competing for access to females. The results supported the argument that hunger can influence the outcome of contests indirectly by increasing an animal's overall 'aggressiveness' or tendency to compete. Thus an internal condition (hunger) appears to affect the spider's tendency to compete irrespective of current contest conditions.

Another factor which influenced the outcome of contests but was unrelated to the current contest condition was body size. Larger spiders (in terms of tibia length) tended to escalate higher than smaller spiders even though these spiders had no previous experience of competing for females.

Many workers when discussing contest behaviour, tend to emphasise the role of current contest conditions and the assessment of these conditions in dictating the outcome of contests (e.g. Englund and Olsson 1990, Riechert 1984). If characteristics such as hunger level and body size affect contests in the manner described above, then animals may not assess current contest conditions to such a large extent.

INTRODUCTION

Hunger is the motivation to feed. Hunger, though, can also affect other aspects of an animal's behaviour, such as its chances of winning intraspecific competition. For example a hungry animal will often compete more vigorously for food than a satiated animal (Barnard and Brown 1983, Hazlett et al 1975). This effect of hunger makes adaptive sense as the value of the desired resource (food) is greater for the hungrier animal, thereby increasing the 'cost' (in terms of strenuous competition) that the hungrier animal is prepared to pay for the resource. By facilitating the acquisition of food by a hungry animal, hunger has a functional effect on intraspecific competitions.

However, hunger could also influence competition by increasing an animal's overall aggressive level (i.e., its tendency to engage in contests) for any resource. If this occurs, then current contest conditions would have little or no bearing on the outcome of the contest. Instead, an animal would respond towards a competitor as a direct consequence of its own internal state. The influence of hunger on these intraspecific competitive interactions would defy an immediate functional explanation and might appear non-functional.

Previous studies of the effect of hunger on contests have examined both functional and non-functional explanations. Barnard and Brown (1983) looked at the functional effect of hunger. They found that when two shrews occupied the same territory, the shrew that obtained less food in the territory won more disputes. They attributed this to the different perceived values of the resource to the individuals, saying that retaining the territory was more important to the hungry animal than the satiated one because it was of more value to the hungry animal.

Work that has looked at the 'non-functional' effect of hunger (which is whether hunger increases the overall 'aggressiveness' of the animal) has had mixed results. For example, Hazlett et al (1975) found that in a

crayfish, *Orconectes virilis*, hungrier individuals tend to be more aggressive. Hunger is also reported to increase intraspecific aggression in a slug, *Hermissenda crassicorni* (Zack 1975). However, because these animals are cannibalistic, they may have been behaving in a predatory, as well as strictly aggressive, way towards each other. In addition, Da Silva Nunes (1988) found that hunger does not increase overall aggressiveness in male salamanders. Instead, male salamanders fed small amounts of food showed more avoidance behaviours than salamanders fed large amounts of food and which were more aggressive.

If hungrier animals do have an advantage in contests against satiated animals, then interpretation of this must consider a conflicting factor: weight gained by satiated animals through feeding may also affect the outcome of the contest. Large body size is well documented as having a major influence on the outcome of contests and the advantage of size has been reported in a wide spectrum of animals (see Archer 1988 for a review). Body size is often gauged by both measuring body length and body weight (Riechert 1984, Faber 1989). If large size is as dominant in controlling outcomes in contests as the literature suggests, then the weight gained from feeding may actually increase rather than decrease the chances of winning by recently-fed animals.

I looked at the effects of feeding on contests of *Argyrodes antipodiana* (O.P. Cambridge). *A. antipodiana* is a small (body length c. 3mm long), kleptoparasitic spider which normally lives in small groups on the webs of a larger host spider, *Eriophora pustulosa* (Walck) (Whitehouse 1986), from which it steals food. Male *A. antipodiana* are known readily to contest for female webs (Chapter 4). Males range in weight from 1 mg to 4 mg, and individual males are capable of doubling their weight in a few days when provided with ample food (pers. obs.). As *A. antipodiana* has simple eyes and presumably only limited abilities for acute vision (see Homann 1971), vibratory displays and possibly pheromones are expected to

be the main form of communication in these spiders. As a heavier spider moving on a web presumably produces stronger vibrations than a smaller spider, then in contests where animals assess each other's size through vibrations, heavier spiders may be at an advantage.

In this chapter I examine the effect of manipulating weight and hunger on contests between *Argyrodes antipodiana* males. The aim is to test whether hunger increases a male's chances of obtaining access to a female independent of the influence of weight.

MATERIALS AND METHODS

Maintenance in the Laboratory

Spiders were collected in Te Aroha (New Zealand: 37.32°S; 175.43°E) as juveniles or in eggsacs and then reared in the lab on foodbundles caught by another spider, *Achaearanea* sp. (Theridiidae). (*Achaearanea* was removed from the web each time before feeding *A.antipodiana*.) This technique, which is detailed elsewhere (Chapter 2), provided *A.antipodiana* with ready-made meals, and was necessary because *A.antipodiana*, as a kleptoparasitic spider, is very poor at catching flies on its own web (Whitehouse 1988).

This feeding method was preferable to housing *A.antipodiana* with its common host, *Eriophora pustulosa*, as it guaranteed that all *A.antipodiana* that were fed obtained food, that all spiders received a similar amount of food, and that no *A.antipodiana* were lost through being eaten by the host.

A.antipodiana were housed in groups of three until 1-2 moults before maturity at which point they could be sexed and housed separately. By rearing the spiders individually, *A.antipodiana* had no previous encounters with conspecifics as adults. This removed the possibility of past experience influencing the outcome of these contests (Chapter 6).

Measurements of body weight and body size

In order to compare the influence of hunger and weight on male-male contests, it was necessary to measure the animal's size and weight. Spiders were weighed using a Cahn 21 electrobalance. Body size (or body length) was gauged by measuring the tibia of the right leg I with a microscope fitted with an ocular micrometer. Work on other spider species (Jakob and Dingle 1990) shows that the length of the tibia is strongly correlated to the size of other body parts, and so tibia length should be a good indicator of body size.

However, animals with the same body size (i.e. same tibia length) may differ in weight. In these experiments, there were two reasons why spiders may differ in weight. Firstly, the spiders may naturally differ in build, as commonly occurs in humans, or secondly, one animal may have recently fed and so be heavier than the other because it is full of food. In these tests, same-sized animals which differed in weight because of build (all-unfed tests) were compared with interactions between same sized animals which differed in weight because only one had been fed recently (larger-fed tests).

Testing procedure

Interactions were observed for 15 min and were staged on the female's webs (constructed in the small cylindrical containers previously described) with the female present. Males entered the cage by being slowly dropped in on their dragline. They were introduced within 10-20 s of each other. Each male was used in only one test.

Two types of tests were staged: all-unfed and larger-fed. In larger-fed tests, spiders were fed 8 days before the test. Seven days later, spiders were paired by matching both tibia length and body weight. One of the pair (randomly chosen) was then fed on that day; the other was left unfed. The spiders were re-weighed and tested on the following day.

If the re-fed spider increased in weight by less than 10%, I assumed the spider had not fed and the pair was not tested. Any weight differences within pairs in these tests was assumed to be the result of feeding.

In all-unfed tests, spiders were fed 8 days before the test. Seven days later, spiders were paired by matching tibia length only. As these spiders had not been fed for a week, any weight difference within pairs was assumed to be due to natural variation in body weight.

Thus, in all-unfed pairs, weight difference is due to build, whereas in larger-fed pairs, weight differences is induced by feeding. For both all-unfed, and larger-fed tests, the difference in body weight between a pair of spiders was calculated as a percentage of the larger spider's weight.

Analysis of male-male interactions

Male-male interactions were classified into 3 types:

1. One male immediately mated with the female without the males first interacting.
2. Males held a contest with the winner then mated with, or at least courted, the female.
3. Males held a contest without the winner then mated with, or at least courted with, the female during the 15 min test period.

Males held a contest if they displayed at each other (see Chapter 4 for a description of displays). The method used to ascertain which spider was the winner and which was the loser of the contest is the same as that used elsewhere (Chapter 4). Basically, a 'winner' was a spider that predominantly (more than c. 80% of the time) chased the other male (the loser). If no spider predominantly chased the other, no winner or loser was designated.

In type 3 interactions I assumed that the males were contesting for access to the female. A type 3 interaction was 'unclear' if there was no

clear winner of the contest, or if one spider won the contest but the other spider mated or courted the female.

Type 1 interactions were discarded from the analysis.

Behavioural differences

Male-male contests in *A. antipodiana* are known to escalate through stages: 0 stationary, 1 moving or shuddering, 2 touching, 3 grappling, and 4 wrestling. All these behaviours are described in detail elsewhere (Whitehouse in prep., Chapter 4) and will only be described briefly here. *A. antipodiana* shuddered by rapidly vibrating its abdomen. *A. antipodiana* touched when one spider extended its leg I and made contact with the body or legs of the other spider. To grapple, spiders faced each other at about 2mm apart and then extended their legs I and II sideways and opened their chelicerae. They then began to vibrate their bodies rapidly, all the time moving closer towards their opponent until they touched chelicerae, at which point they wrestled by locking chelicerae and grabbing each other with their first two pairs of legs. An *A. antipodiana* bit another when its chelicerae connected with another animal.

RESULTS

Effect of weight difference on the outcome of contests

Out of the 75 tests conducted, 43 were 'all-unfed' and 37 were 'larger-fed'. The difference in body weights for all pairs tested ranged from 3.05% to 42.39%. Larger-fed pairs with a body weight difference of less than 10% were not used. Therefore I decided to also discard all all-unfed pairs with a body weight difference of less than 10% (n=11) leaving a total of 32 all-unfed pairs.

Effect of weight in all-unfed tests.

Of the 32 pairs of all-unfed spiders where the difference in weight was greater than 10%, 4 had interactions that were classified as 'unclear' and 2 had type 1 interactions. Consequently only the tests of 26 pairs (the pairs that had type 2 interactions) could be analysed.

Of the 26 pairs used in all-unfed tests which were analysed, smaller males obtained access to the females in 8 of the tests, while larger males obtained access in the remaining 18 tests. Thus, in the all-unfed tests, the trend was for larger spiders to win the contest, although the difference was not significant (goodness-of-fit test: $\chi^2 = 3.12$, $0.1 < P < 0.05$, $n=26$).

However, by separating the effect of weight into different categories it became apparent that, when the weight difference was greater than 20%, larger spiders in all-unfed tests are much more likely to win contests (test of independence: $\chi^2 = 6.75$, $P < 0.01$, $n=12$, Fig. 1).

Effect of weight in larger-fed tests.

Of the 37 pairs used in larger-fed tests, two were classified as unclear, and seven were type 1 interactions, resulting in 28 tests (the pairs that had type 2 interactions) being available for analysis. Of these, smaller males obtained access to the female in 13 of the tests, while in the remaining 15 tests larger males obtained access. Thus in larger-fed tests, increasing weight by feeding did not increase a spider's chance of gaining access to the female (goodness of fit test: $\chi^2 = 0.04$, NS, $n=28$).

If the effect of weight in these results is separated into different categories, smaller spiders in larger-fed tests still appeared to have an equal chance of winning contests when the weight difference was 20%, but larger spiders appeared to be more likely to win contests when the weight difference was greater than 30% (Fig. 1).

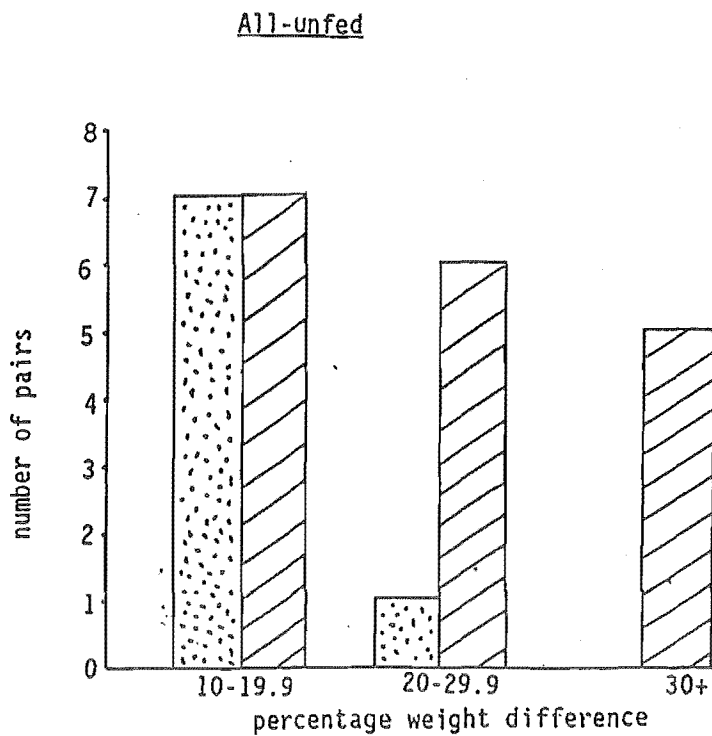
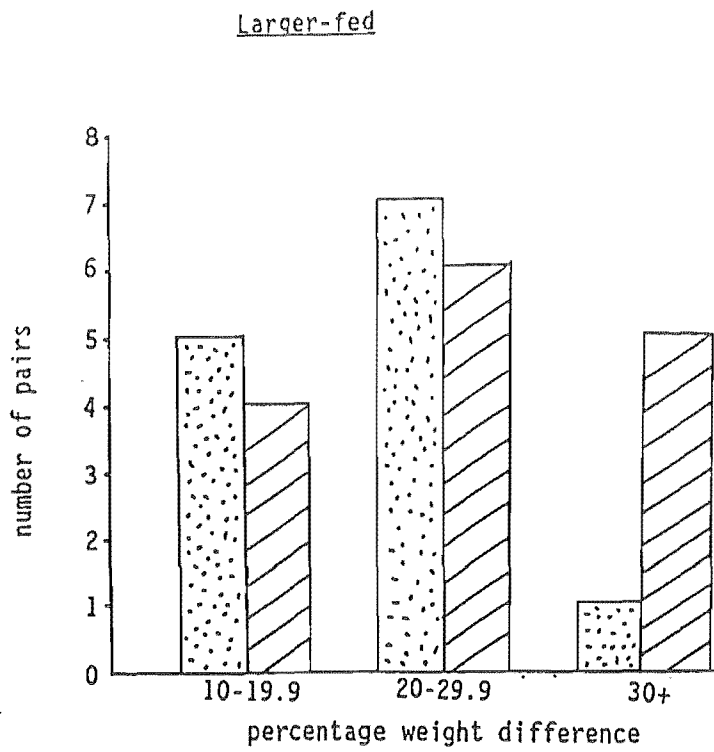


Fig. 1. The percentage weight difference of pairs in larger-fed and all-unfed tests. Stippled bars indicate that the smaller spider in the pair won these contests, while the striped bars indicate that the larger spider won.

Comparison in the effect of weight between all-unfed and larger-fed tests.

Heavier spiders appeared to have an advantage in both larger-fed and all-unfed tests. However, while heavier spiders in all-unfed tests won more interactions when the weight difference was 20%, heavier spiders did not appear to win more interactions in larger-fed tests until the weight difference was 30% (Fig. 1).

The effect of weight was directly compared between larger-fed and all-unfed test groups. 'Small winners' (that is, spiders that were winners but weighed less than their opponent) in the larger-fed tests were proportionally smaller (21.44% smaller on average, s.d.=4.96) than their counterparts (which were on average 15.70% smaller, s.d.=3.10) in the all-unfed group (t-test: $P=0.001$, $n=21$). This indicates that smaller spiders in all-unfed tests could win only when they were just slightly smaller than their adversary, whereas smaller spiders in larger-fed tests could still win contests when they were considerably smaller than their adversary.

Hence the influence of weight on the outcome of larger-fed tests appears to be reduced in comparison to the all-unfed tests.

Contest escalation

In all-unfed ($n=26$) and in larger-fed ($n=28$) tests, most contests escalated to grappling (all-unfed: 85%, larger-fed: 93%) and many escalated to wrestling (all-unfed: 46%, larger-fed: 57%). The time spent grappling ranged from 3 s to over 6 min (mean = 1:20 min, s.d.=1:21 min). The two groups did not differ significantly in either the length of time spent grappling (Mann-Whitney U test: NS, $n=41$), or the proportion of interactions that escalated to wrestling (test of independence: $\chi^2=0.28$, NS, $n=54$). Nevertheless analyses were conducted to see if the level of escalation was correlated with either weight difference within a pair, or body size (as gauged by tibia length) within a pair.

Escalation as measured by grappling.

Twenty three larger-fed pairs and 18 all-unfed pairs escalated to grappling. The length of time larger-fed males spent grappling was not correlated with either tibia lengths or percentage size difference (linear regression: NS, d.f.=18, Fig. 2). The length of time all-unfed males spent grappling was also not correlated with either tibia length or percentage size difference (linear regression: NS, d.f.=15, Fig. 2).

Escalation as measured by biting.

Body size (as gauged by tibia length) of all-unfed and larger-fed pairs did have some bearing on tendency to escalate to biting. By chance, spiders used in larger-fed tests had slightly larger tibia than those used in all-unfed tests (Mann-Whitney U test: $P < 0.05$). Concurrently, body size had the strongest influence in larger-fed tests in that spiders with larger tibia were more likely to wrestle than spiders with smaller tibia (Mann-Whitney U test: $P = 0.03$). The same trend was suggested by data in all-unfed tests, although the result was not significant (Mann-Whitney U test: $P = 0.09$).

The percentage weight difference within a pair did not appear to affect the likelihood of a spider biting in larger-fed tests (Mann-Whitney U test: NS), although there was a trend of weight difference affecting a pair's tendency to bite in all-unfed tests (Mann-Whitney U test: $P = 0.08$) where pairs which were similar in weight were more likely to bite.

Possible influence of female choice

Conceivably, female choice may have influenced results of these tests, especially if females preferred heavier or hungrier males. Out of the 75 tests conducted, there are only 2 cases where the female, who was between 2 courting males, may have shown a preference towards a male by moving towards it. However, 1 of these interactions was classified as

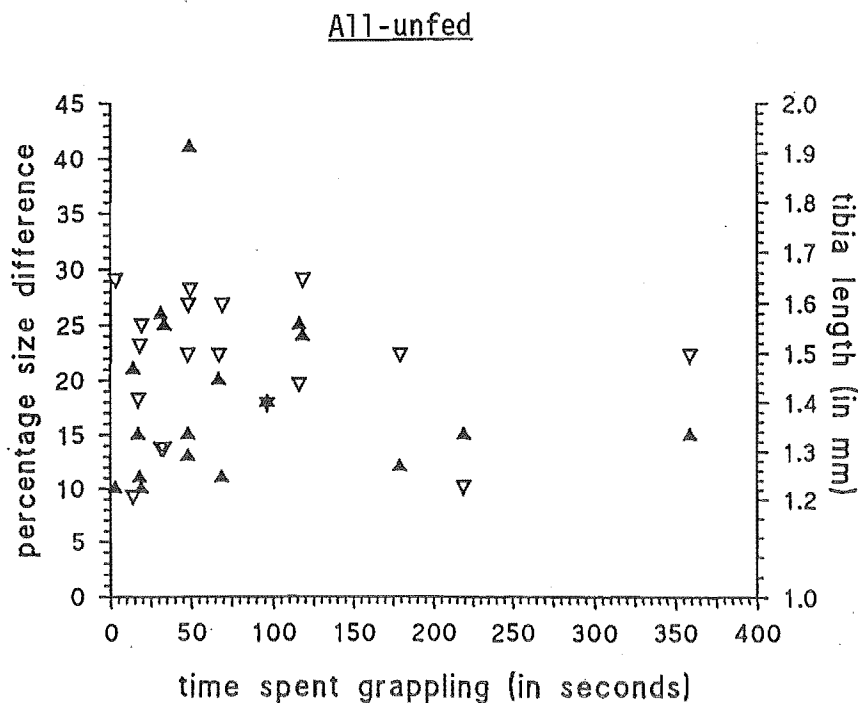
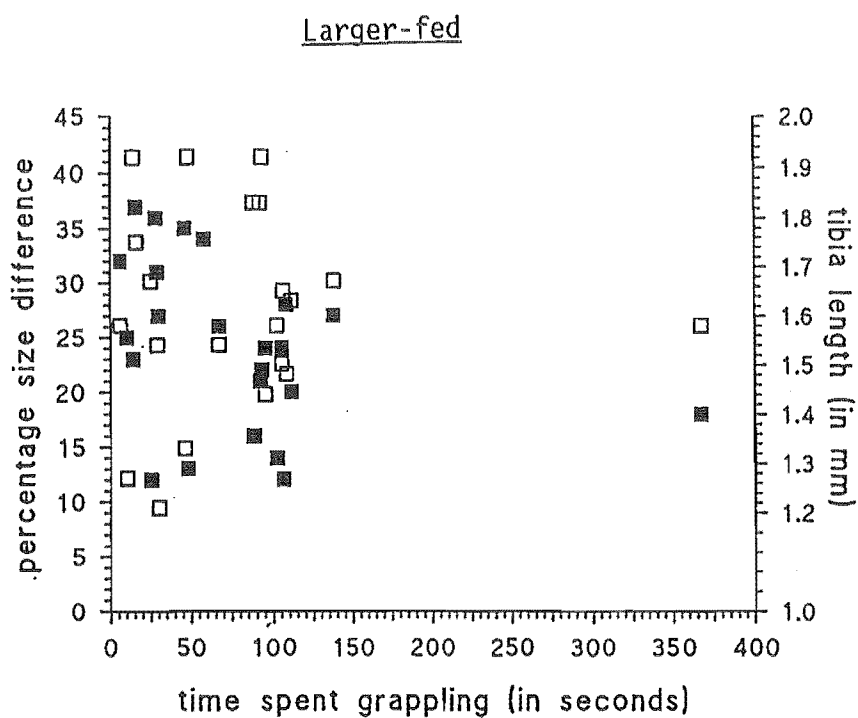


Fig. 2. The relationship between time spent grappling and both the percentage size difference between the pairs (shaded shapes) and the average tibia length of the pair (clear shapes). Grappling did not correlate with these 2 factors in neither the larger-fed tests nor the all-unfed tests (larger-fed: NS, d.f.=18; all-unfed: NS, d.f.=15).

'unclear' and the other was classified as a type 1 interaction, so neither affected results as they were not included in the analysis.

DISCUSSION

Characteristics of naive contests

This chapter provides information on the fighting behaviour of naive male spiders. A characteristic of these contests was their high degree of escalation which was much greater than that seen in other male-male contests in which the female was present (e.g. Chapter 6). Naive animals are often thought to have the behavioural characteristics of dominants (e.g. Hazlett et al 1975). Thus animals which win contests do not, with experience, become more likely to escalate as they win more contests. They simply retain their original tendency to escalate. The high level of escalation in the contests reported here supports the argument that naive animals behave like dominants.

Another interesting characteristic of the interactions was that encounters between large males (as indicated by tibia length) were more inclined to escalate to biting than those between small males. This effect of body size has also been reported in other spiders (Faber 1989). As the *A. antipodiana* used in these tests were naive, the effect of actual body size on aggressiveness may be innate. This possibility has major implications to contest behaviour. That is, large spiders may innately escalate higher than smaller spiders, irrespective of the current contest conditions or of their own past experience.

The possible influence of hunger on contests

In the results presented here, a hungry, lighter male appeared to have a better chance of winning the contest if its opponent had recently fed than if it too was hungry. When hunger was not a factor, heavy and light spiders had an equal chance of winning contests up to a difference

in weight of 20%. When the weight differential was greater than 20% most contests were won by heavier males. However, when hunger levels were uneven, light and heavy spiders appeared to have about an equal chance of winning right up to a difference in weight of 30%, but above 30%, heavier spiders again predominantly won. Thus the weight advantage appeared to be less in the tests where the larger spider had just eaten, and the smaller spider was hungry, suggesting that hunger may affect an animal's motivation to contest resources, irrespective of what the resource is.

However, before this conclusion can be accepted, other possible explanations must be explored. For example, recently fed males may be more sluggish and less inclined to contest resources. That is, smaller spiders in the larger-fed tests may be more likely to win contests because their heavier opponents were more sluggish as a consequence of having recently fed. This explanation was not supported on two grounds. First, there was no difference in the level of escalation attained by the two test groups. If recently fed spiders were more sluggish, one would predict that larger-fed contests would have been shorter, or would not have escalated as highly as the all-unfed contests. Secondly, as the spiders ate more, they would presumably become more sluggish. Thus one would predict that the very much heavier spiders in the larger-fed tests would have been more likely to lose. The results suggest that much heavier spiders were actually more likely to win, and so the results do not support this argument.

Another alternative explanation is that the difference in results between larger-fed and all-unfed tests may occur because a weight increase, induced by feeding, may have no effect on the outcome of contests. Consequently, you would not expect to see weight having any effect in large-fed tests. This conclusion was not supported because larger spiders in half-fed tests appeared more likely to win contests if they were over 30% heavier than their opponents. If weight increase

induced by feeding had no effect, this advantage would not occur.

Consequently, it appears that 'hunger' may increase the spider's 'competitiveness' in general - irrespective of what the animal is competing for. This has major implications. When workers observe contests they usually relate the behaviour of the animals to the conditions of the contest (e.g. Englund and Olsson 1990, Riechert 1984). But, if internal motivational factors in the competing animals are particularly compelling, then the behaviours observed in the contest may actually have little to do with either what the animals are competing for or with the characteristics of the opponents. In fact it may even be erroneous to try to relate the observed behaviours of the competitors to the current contest conditions.

CHAPTER 6

The influence of past experience on a male's motivation to fight in the spider *Argyrodes antipodiana* (Theridiidae: Araneae)

ABSTRACT

It is well known that past experience influences the contest behaviour of vertebrates (e.g. Hazlett et al 1975). However, relatively little work has been done on the effect of past experience on the contests of invertebrates (but see Otronen 1990, Ewing 1967). Here I provide evidence which indicates that past experience influences the outcome of contests between males of the spider *A. antipodiana* for access to females. I found that the males which had had previous experience of winning contests were more likely to win contests against males which had had previous experience at losing contests.

INTRODUCTION

When an animal enters into a contest, it is often faced with a very complex situation (Chapter 9). This is because many factors may be operating at any one time which could influence the relative RHP (Resource Holding Power; sensu. Parker 1974) of the contestants. Examples are the relative size of the competing animals, whether one animal 'owns' the contested resource, and whether the value the two animals place on the resource differs (see Archer 1988 for a review). To assess accurately the RHP of its opponent in relation to its own RHP, an animal should assess all relevant factors.

An animal might simplify the situation by reducing the amount of assessment it carries out in order to gauge the abilities of its opponent. That is, an animal might use a 'rule of thumb' for making decisions: paying attention to only a limited numbers of factors instead of basing decisions on a more complex and complete array of factors. Basing decisions on past experience may enable an animal to usually gauge accurately enough the relative RHP of itself in relation to its opponent, and thus avoid the need to assess RHP precisely.

According to predictions derived from game theory, if two animals within a closed population compete for a resource, the animal with the higher RHP will win the contest (Maynard Smith 1976). As an animal takes part in more contests, the proportion of its wins and losses will theoretically begin to reflect the position of its RHP in relation to the rest of the population. Hence, after numerous contests, an animal could predict reasonably well its chances of winning a current contest on the basis of how well it did in past contests. Memory of past contests might provide an animal with a crudely accurate way of predicting how likely it is to win or lose a current contest, without requiring an ability to assess the RHP of its current opponent precisely. Although only crudely accurate, decisions based on memory of past contests may give the animal a high a degree of accuracy as it normally needs. The advantage of this crude method is that it means that an animal could more or less ignore the RHP of its current opponent and simply respond to the opponent in the manner dictated by its past experience, thereby greatly simplifying information processing during contests.

That past experience can influence contests is well known for vertebrates such as mice (Rasa and van den Hoovel 1984) and fish (Abbott et al 1985, McDonald et al 1968, Frey and Miller 1972, Francis 1983, Franck and Ribowski 1987, Beacham and Newham 1987). There are also examples from insects such as cockroaches (Ewing 1967), crickets

(Alexander 1961), burying beetles (Otronen 1990), and fruitflies (Hoffman 1990).

Whether past experience influences contests in spiders is not so clear. The only previous study related to this question appears to be on a linyphiid spider, *Frontinella pyramitela* (Suter and Keiley 1984). In this species, winning per sae, did not affect the male's chances of winning in subsequent contests.

I carried out a study on how past experience influences contests in *Argyrodes antipodiana* (O.P. Cambridge), a small (body length: c.3mm) kleptoparasitic spider from New Zealand. *A. antipodiana* tends to live in small groups of c. 4 adults around the webs of the orb weaver *Eriophora pustulosa* (Walck) from which it steals 'foodbundles' and off whose web it gleans small insects. Male *A. antipodiana* are capable of distinguishing between male and female silk (Whitehouse in prep.), they actively move between foraging groups (Chapter 1) and they readily compete with each other for access to females (Chapters 4 and 5).

The aim of this paper is to see whether male *A. antipodiana* with past experience of losing contests for females are more likely to lose against males of a similar size that have had past experience of winning contests for females.

MATERIALS AND METHODS

Maintenance in the Laboratory

A. antipodiana was collected in Te Aroha (North Island, New Zealand) as juveniles or eggs, then reared in the laboratory on 'foodbundles' caught by another spider, *Achaearanea sp.* *Achaearanea sp.* was removed from the web each time before feeding *A. antipodiana*. This technique, which is detailed elsewhere (Chapter 2), provided *A. antipodiana* with the equivalent of 'pre-cooked TV dinners', and was necessary because *A. antipodiana*, as a kleptoparasitic spider, is very poor at catching flies on its own web

(Whitehouse 1988). Housing and feeding *A.antipodiana* in this manner was preferable to housing *A.antipodiana* with its common host (*Eriophora pustulosa*) because it guaranteed that: firstly, every time I tried to feed *A.antipodiana* it, rather than the host, obtained the food; secondly, each *A.antipodiana* received a similar amount of food; and thirdly, no *A.antipodiana* was lost through being eaten by the host.

A.antipodiana was housed in groups of three until 1-2 moults before maturity after which they it was sexed and individuals housed separately. This prevented *A.antipodiana* from having impromptu interactions with conspecific subadults. However, all animals used in this test had been involved in one male-male contest as an adult.

Training

The training sequence used is summarized in Fig. 1. Spiders were weighed using Cahn electrobalance and the tibiae of their right legs were measured using a microscope fitted with an ocular micrometer. Spiders were then marked with small dot fluorescent paint on the cephalothorax so that members of a fighting pair could be easily distinguished.

A total of 110 males were used in these tests, ranging in tibia length from 1.00mm to 1.96mm and in wet body weight from 0.98mg to 2.43mg. Body weight varies substantially depending on whether the spider has recently eaten (Chapter 5). Therefore, body weight could be used only as a rough indication of true size. Of the 110 spiders, 38 were 'small' spiders (tibia length 1.00mm to 1.50mm) used to train winners; and 34 were 'large' spiders (tibia length 1.63mm to 1.96mm) used to train losers. The remaining 38 were the test spiders (tibia length 1.42mm to 1.71mm).

Test spiders were assigned to pairs, each member of the pair being similar in size; tibia lengths differed by no more than 0.04mm (3% of tibia length) and body weight differed by no more than c.15%. One spider from each pair was randomly chosen to be trained to be a winner and the

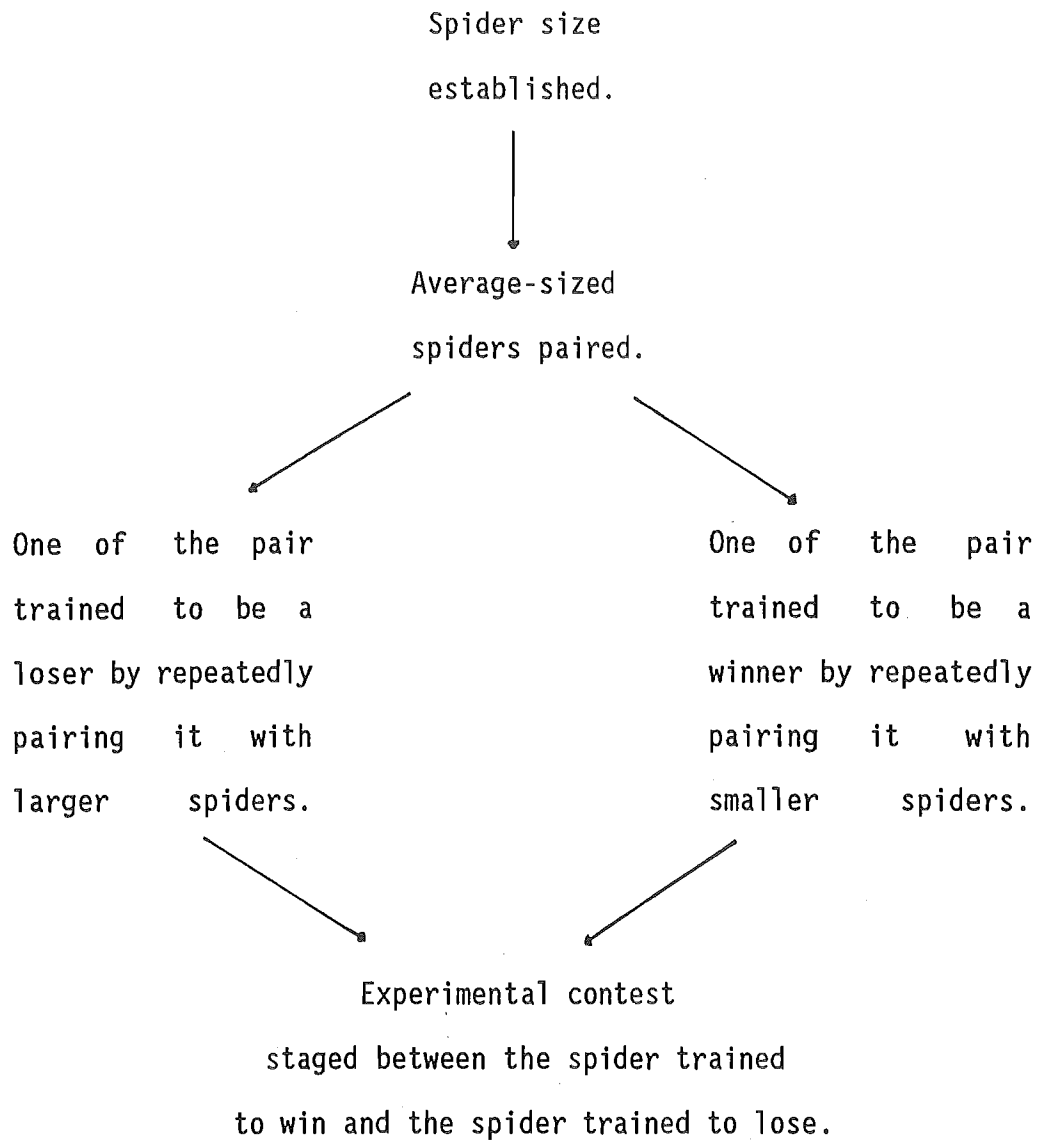


Fig. 1. The sequence of events used to train spiders in preparation for the experimental contest between spiders trained to win and spiders trained to lose (see text for more details).

other was trained to be a loser.

It is known that when there is a substantial difference in size of spiders, the larger spider tends to win (Chapter 5). Therefore, to train a spider as a 'winner', it was subjected to training sessions with smaller spiders. Similarly, to train a spider to be a loser, it was subjected to training sessions with larger spiders (Fig. 1). A spider was referred to as 'trained' when it won (or lost) 8 consecutive sessions.

A spider was judged to be the 'winner' if it fast grabbed at the other spider (see below). Previous work has shown that fast grabbing is a reliable indicator that a winner has been established and the contest is over (fast grabbing was shown to be 97.3% accurate in indicating the winner of a contest, $n=151$, Chapter 4). If no spider fast grabbed, the 'winner' was the spider which most often (>80% of the time) caused another spider (the loser) to move away from him. If no spider fast grabbed and both spiders moved equally often towards or away from the other, no winner or loser was recognized.

Training session

Training was staged in small (50x50mm) plastic cylindrical cages containing a web which had been occupied recently by a female (males are known to be able to distinguish between male and female silk; Whitehouse in prep.). To carry out training, two males were put into the cage and allowed to interact until a winner was established. Sometimes during training males were reluctant to compete. Apparently this was because they habituated to the setup. When this happened, a female was added to the cage to encourage interactions. Test spiders were trained 2 to 3 times a day with at least 2 h between each session, resulting in a total of c.12 training sessions per spider and 475 sessions in all.

Experimental contest

The contests, like the training sessions, were staged in small cylindrical cages containing a recently vacated (female removed no more than 5 min earlier) web of a female. Contests were staged between trained winners and trained losers who had been chosen at random for the contest and assigned for one of the two training regimes at random (Fig.1). The males were added to the cage within 10 s of each other, and were left on the web for 10 mins, during which time I recorded their behaviour. Contests were observed 'blind', in that a colleague re-labeled the trained winners and losers so that I did not know, during any particular test, which male was which. Contests were staged the day after the last training session.

Behavioural analysis

Descriptions of behaviours.

All behaviours used by these animals are described in detail elsewhere (Chapters 4, Whitehouse in prep.) and will be described only briefly here. *A. antipodiana* shuddered by rapidly vibrating its abdomen up and down. One spider touched another by extending a leg I and making contact with the body or legs of the other spider. Spiders faced by orientating their cephalothoraces towards each other. Spiders dropped by suddenly "leaping" off the web and hanging by their dragline. Spiders walked across the web to move towards or move away from each other. To grapple, spiders faced each other while about 2 mm apart, then extended legs I and II sideways and opened their chelicerae. They then began to vibrate their bodies rapidly, all the while moving closer towards their opponent until their chelicerae touched. Next, they wrestled by locking chelicerae and grabbing each other with their first two pairs of legs (see Chapter 4). Sometimes a male suddenly lunged (described in Whitehouse 1986) by propelling itself towards a target and simultaneously trying to

scoop the target towards its mouthparts with legs I. In this study, only lunges where the chelicerae made contact with the opponent were recorded. Therefore in this study, all lunges were terminated with a bite. The usual definition given for 'biting' is that one spider makes contact with another spider with its chelicerae (Chapter 2). However, in this Chapter, for ease of reference, both 'biting' and 'wrestling' were collectively called biting.

To fast grab, a spider pulled quickly with its legs I and II on the dragline of the other spider, hauling in the silk. Spiders did slight leg movements by moving any combination of their legs very slightly (c. 0.5 mm) and randomly. Contests escalated through shuddering and moving to touching, then grappling and, occasionally, wrestling (Chapters 4 and 5).

The possibility that *A.antipodiana* reveal their intentions to conspecifics.

When animals compete they sometimes reveal, through their displays, how much effort they are willing to invest in attempting to win the contest (e.g. Poole 1989). My study allowed me to look for this with *A.antipodiana*. If the paired spiders behaved differently prior to a winner or loser being established during the test, then this may indicate that these spiders are revealing their intentions to each other.

The first step towards establishing whether they behaved differently was to define at what point during an interaction a winner was established. Two criteria were used to ascertain the winner of the contest; 1) which spider 'fast grabbed', and 2) which spider usually displaced the other. In contests where fast grabbing occurred, only the behaviours that occurred before the first incidence of fast grabbing were compared. In the contests where a 'winner' was determined by one spider usually displacing the other, all recorded behaviours, were analysed.

To establish whether winners and losers behaved differently, behaviours performed by the two trained animals in the experimental contests were compared. If a behaviour was performed by only one spider during the course of the interaction, irrespective of how many times it was performed, the behaviour was attributed to that spider. If the behaviour was performed by both spiders at some stage in the interaction, both spiders were credited with the behaviour, even if one animal performed it more frequently than the other.

RESULTS

Of the 19 pairs trained, 17 were used in test fights. Of these, 16 held contests in which one spider clearly won and the other clearly lost. In 3 interactions one spider fast grabbed at the other. In the remaining 13 tests, one spider usually (>80% of the time during the interaction) moved towards the other and the other spider moved away. The result of one interaction was unclear, because the spiders did not clearly move towards or away from each other and no spider fast grabbed. This is despite the fact that one spider dropped away from the other (therefore behaving like a loser) while the other continually shuddered as it moved over the web (therefore behaving like a winner). Thus, although the trained winner and loser in this test appeared to 'win' and 'lose' the interaction, respectively, the test did not meet the criteria established for clearly identifying a winner and loser, and so could not be used in this analysis, even though the interaction was used in the behavioural analysis below.

Does prior training affect the outcome of aggressive interactions?

Of the 16 tests where winners and losers were clearly identifiable, the trained winner won and the trained loser lost in 15 tests, whereas in one test the trained winner lost and the trained loser won (test of goodness of fit, $\chi^2=10.56$, $P<0.005$). The test where the winner lost and

the loser won was one of the two tests in which the spiders escalated through to grappling. In this test, the pair grappled for 1:09 min before the trained winner finally lost. These results indicate that training strongly influences the outcome of contests.

Two pairs were not tested because in each case one spider continued to behave as a loser despite attempts to train it as winner. However, if these pairs are included in the analysis as "failed tests", training still strongly influences the outcome of contests ($\chi^2=6.72$, $P<0.01$, $n=18$).

Level of escalation

Of the 475 training sessions, spiders grappled in 75 (15.8%) and bit each other in 40 (8.4%). Of the 47 initial training sessions, 21 (44.7%) escalated to grappling while 3 (6.4%) involved biting. Test contests did not escalate to such a degree, with only 2 out of 18 (11%) included grappling and none incurring biting. A test of independence was done comparing escalation to grappling in the initial training contests with the final test contests, and it was found that spiders escalated to significantly higher levels in the initial training contests ($\chi^2=5.03$, $P<0.0025$, $n=65$).

Do males reveal their intentions to their rivals?

In total, 11 behaviours were recorded in contests between trained males (Fig. 2). Three of these behaviours (move towards, fast grab and move away) were used to identify winners and losers. A McNemar test of significance of change (with Yate's correction) revealed that within experimental contests some behaviours were significantly more likely to be performed primarily by winners while others were performed primarily by losers. Two of these, alert and dropping, were performed significantly more often by losers than by winners (alert: $\chi^2=8.1$, $P<0.005$, $n=13$; drop: $\chi^2=6.13$, $P<0.05$, $n=8$) while shuddering was more likely to be performed by

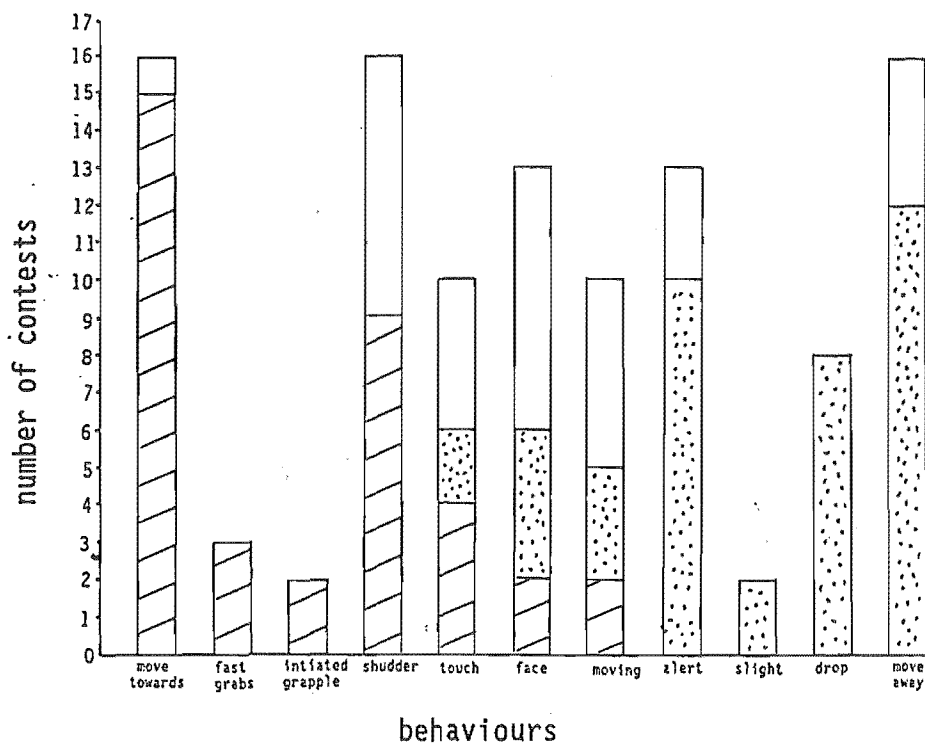


Fig. 2. Behaviours performed during experimental contests prior to the identification of the winner and loser (but including fast grabbing). The histogram indicates whether winners (hatched shading) losers (stippled shading) or both (clear) performed a behaviour during a test.

winners ($\chi^2=7.11$, $P<0.05$, $n=16$). Even in tests where both spiders shuddered ($n=7$) the loser would only shudder once at the beginning of the interaction while the winner would shudder throughout the interaction; again empathizing that shuddering was predominantly performed by winners.

DISCUSSION

How past experience may influence contests

Results here imply that past experience affects the subsequent behaviour of the spider *Argyrodes antipodiana* and that these effects are apparently long term (at least 12 hours).

Exactly how past experience influences contests is unclear. However, McDonald et al (1968) has suggested that the modification of behaviour through experience may be caused by social interactions, which he called 'social conditioning'. He argued that 'experiencing winning' is a positive reinforcement, while 'experiencing losing' is a negative reinforcement. Following this argument, winners (or dominant individuals) should be more inclined to fight than losers (or subordinate individuals). Franck and Ribowski (1987,1989) criticized this interpretation. They discovered that, in long term stable hierarchies in fish, high ranking males are actually much less aggressive against a new competitor than low ranking males. This result appears inconsistent with the social conditioning hypothesis of McDonald et al (1968) and led Franck and Ribowski to conclude that the hypothesis of McDonald et al was not very useful in explaining how past experience operates.

In contests between male *A. antipodiana* there was little evidence that dominant individuals (defined here as winners) were more inclined to fight. Very few of the behaviours seen in contests were distinct displays as such, and few contests between trained spiders resulted in an escalation to grappling. Shuddering was the most commonly used display, but it was most likely directed at the female rather than at the other

male. Thus the results here, like those of Franck and Ribowski (1987, 1989) do not support the proposal of McDonald et al 1968 that past experience influences contests through social conditioning.

Another means by which past experience may influence contests is by altering an animal's motivation to compete by altering its 'expectation' in a contest. For example an animal accustomed to winning may 'expect' to win when it encounters another animal and may 'expect' the other animal to back down. This effect could explain why, in both fish and mice, dominant animals were less aggressive while lower ranking animals were more aggressive. That is, the lower ranking animals may "expect" to need to fight if they are going to attain the resource.

If past experience influences contests by altering an animal's expectations, then this may explain why there was so little escalation in the contests of *A.antipodiana* in the present study. Winners may not have expected their opponent to be a threat, and therefore concentrated their efforts on locating the female (by shuddering); in contrast, the loser, after locating its opponent, may simply have kept out of its way, waiting for a chance to sneak copulations later (Chapter 4).

Indicating intentions

The behaviour of the *A.antipodiana* males that won contests was significantly different from the behaviour of the males that lost interactions. This goes against a prediction (derived from game theory) that animals do not reveal their intentions to rivals (Maynard Smith 1974 Caryl 1979) but is consistent with other studies in which animals have been found to reveal intentions (e.g., Dow et al 1976, Turner and Huntingford 1986, Franck and Ribowski 1989, Poole 1989).

However, in the case of the contests of *A.antipodiana*, game theory analysis may not be applicable. An assumption in game theory is that animals are assessing each other during contests. In the contests of

A. antipodiana, very little assessment of the opponent may have actually occurred as very little escalation occurred during the tests.

The role of assessment and past experience in animal contests

Disadvantages of assessment.

Many workers emphasise that assessment plays an important role in animal contests (e.g., Riechert 1984, 1986). I agree that assessment is an important part of animal contests (see Maynard Smith 1976), but the importance of assessment may be over-emphasised in some instances. For example, animals are often assumed to be capable of assessing and comparing any number of complex and subtle characteristics of themselves and their opponents (e.g. Enquist et al 1990). However, because assessment is a very complex process (Chapter 9), assessment may be too difficult for many animals to carry out.

Assessment can also be costly. Animals that are continually 'assessing' each other by holding contests that escalate, experience a lot of stress. For example, stags competing for access to does quickly become fatigued as a result of the many assessment bouts of roaring and fighting (Clutton-Brock and Albon 1979). Mice too illustrate the costs of continual assessment. Rasa and van den Hoovel (1984) showed that male mice subjected over a long time period to repeated aggressive attacks die of uraemia (kidney malfunction) due to stress. Another example is the cockroach, *Nauphoeta cinerea* whose fighting behaviour to establish dominance/subordination relationships resulted in the death of some subordination animals, apparently as the result of stress (Ewing 1967).

Animals such as cockroaches live in groups and may therefore be involved in many contests. Consequently, they may be particularly inclined to incur high amounts of stress through partaking in contests and bouts of assessment. Thus a means of avoiding such escalated contests may be especially important to group-living animals.

Advantages of past experience.

Using past experience to dictate a response to current contests would be very advantageous to an animal because past experience would mimic assessment without the associated disadvantages.

When using past experience, animals respond to current contests on the basis of how well they did in past contests. These initial contests may have been decided by some form of assessment. As animals that have initial competitive advantages (such as being large) usually retain this advantage, animals that have won contests in the past would have a good chance of winning contests in the future. Thus the initial contests may be decided by assessment, but in later contests the role of past experience may become more important.

This point is well illustrated when it 'goes wrong' (Abbott et al 1985). Abbott et al (1985), while working on inexperienced, young fish, found that the larger fish usually won. This is a common result when animals assess each other during contests, as RHP is often thought to be related to size. Abbott et al (1985) then fed the smaller fish at a faster rate than the larger one until it was much larger than the fish that had initially won. On subsequent pairings, the originally dominant fish still won even though it was now much smaller than its adversary. Thus these animals, as a result of their initial interactions, had become so set in their responses towards each other that the current abilities of the animals seemed to be more or less irrelevant. A response that was initially the result of assessment, had apparently become "hardwired" (sensu Johnston 1985) to the extent that current assessment became irrelevant.

In most situations, contests decided by past experience would agree with those decided by current assessment. That is, in the normal course of events, the larger fish which won the contests when the fish were young would also be the larger fish as adults, and so would still normally win

interactions. However, if the normal course of events had been allowed to take place, then it would have appeared that the adult contest had been decided by assessment when in reality it may be largely decided by past experience.

This brings us to another point about the role of past experience in contests. Contests that appear to be 'decided' by assessment may actually be 'decided' by the animals basing their behaviour on past experience. In many contests, characteristics used in assessment such as size, are good predictors of which animal will win the contest (see Archer 1988 for a review). Consequently, many workers assume that in these contests the opponents are assessing each other's RHP (e.g. Wells 1988). However, many of these contests may not be based on current assessment, but may be largely based on these animal's past experiences. Because the larger animal won in the past, it may 'expect' to win in the current contest: it may not actually 'assess' its current opponent at all. Perhaps past experience has a more important influence in animal contests than is presently apparent.

SECTION III

Behavioural plasticity in feeding techniques

CHAPTER 7

Spiders learn to be thieves and murderers:

The ability of *Argyrodes antipodiana* to improve common (kleptoparasitic) and uncommon (araneophagic) foraging behaviours.

ABSTRACT

In this chapter I look at the ability of *A. antipodiana* to modify common (kleptoparasitic) and uncommon (araneophagic) foraging behaviours. I found that although the kleptoparasitic abilities of *A. antipodiana* were largely innately determined, *A. antipodiana* seemed to use learning to solve problems related to reaching food at the hub. However, development of the uncommon foraging technique, araneophagy, did not seem to require learning. Instead, *A. antipodiana* seemed to have a 'critical period' of exposure. It seemed that if *A. antipodiana* practised araneophagy during this critical period it was able to retain its ability to capture spiderlings, but if it did not use araneophagy during this time it lost its uncommon foraging behaviour.

INTRODUCTION

For animals that live in unpredictable environments, an ability to adjust behaviour to changing conditions might be beneficial. An effective means by which an animal can modify its behaviour is through learning. Learning can be defined as "any process in which the organization of an animal's behaviour is, in part, determined by some specific prior experience" (Chapter 8).

Although an ability to learn can obviously be advantageous, too heavy a reliance on learning, may not always be advantageous (Johnston 1982). For example, an animal with constraints on what it can learn may be at an advantage because it screens out misleading associations, and is able to focus its attention on relevant information in its environment (Johnston 1982).

One means by which learning can be channelled is through 'critical periods' where learning is only possible within a small window of time. For example, many species of birds can learn songs only during a restricted period of time. If these birds do not hear their own species' typical song during this time, they can not develop their song (Baptista and Petrinovich 1986). A similar phenomenon occurs in the acquisition of vision by cats. Cats have a critical period from the second to fourth month after birth. If a cat has one eye covered during this period, it is effectively blind for life in that eye even if this eye is later uncovered (Aoki and Siekevitz 1988).

Although most work on learning has been concentrated on vertebrates (e.g. Roper 1983, Johnston 1985), there has been a recent increase in interest in learning by invertebrates (e.g. Hodos 1982, Griffin 1985). Much of the research on invertebrate learning has focused on foraging and, in particular, the ability of insects to choose between different food types. In these studies, it has been shown that past experience is an important influence on the behaviour of insects. For example, past experience can modify a caterpillar's preferred choice of food (*Rhagoletis pomonella*: Papaj and Prokopy 1986) and can also influence a female insect's choice of plant upon which either to oviposit (*Rhagoletis pomonella*: Prokopy et al 1986) or to look for prey (*Diaeretiella rapae*, a wasp that is a parasitoid of aphids: Sheehan and Shelton 1989). Moreover, past experience can modify the behaviour of a male insect by influencing its choice of a plant with which to associate (*Drosophila melanogaster*:

Jaenike 1988).

Many insects are able to change their food preferences throughout their lives. Others are predominantly influenced by conditions they encounter when young, and particularly as soon as they emerge as adults (Jaenike 1988). The ability of insects to modify their plant preferences thus appears to be age dependant, although there has been no report that these restrictions are evidence of "critical periods" in the sense discussed for the acquisition of a bird's song or a cat's vision.

Most of the current work on how learning influences foraging behaviour in invertebrates (e.g., the slug *Limax maximus*: Gelperin 1989), deals with altering choices between food-types rather than examining whether the feeding behaviour itself can be modified. An important exception is the honeybee (e.g. Menzel 1989).

In the work presented here, experiments were designed to examine whether the actual behaviour patterns used by *Argyrodes antipodiana*, a kleptoparasitic spider, during foraging can be modified with experience.

Argyrodes antipodiana is a small (body length 3 mm) spider with diverse foraging methods. *A. antipodiana* feeds primarily by kleptoparasitizing the webs of larger orb-weaving spiders. It does this by concentrating on a limited number of host species, then employing numerous kleptoparasitic techniques. These include: stealing food that the host has caught and wrapped by hauling these 'foodbundles' out of the host's web; feeding directly on small insects caught in the host's web but 'ignored' by the host; and moving directly onto the host's web and feeding off the same foodbundle upon which the host is feeding without being detected by the host. However, *A. antipodiana* can also feed araneophagically on the host when the host is moulting (and therefore vulnerable), or also prey on small spiders on other species.

The aim of this paper is to examine whether learning is involved in two of *A. antipodiana*'s feeding methods: feeding with the host and

capturing spiderlings.

This paper is divided into two sections. The first section examines whether *A.antipodiana* can improve with practise its ability to catch spiderlings (in this case young *Achaearanea*) and if so, whether this ability is modifiable throughout the animal's life or limited to a critical period. The second section examines whether *A.antipodiana* is able to improve its ability to feed with the host *Eriophora pustulosa* with practice.

GENERAL METHODS

Maintenance

A.antipodiana were collected from Te Aroha, (North Island, New Zealand) and used as laboratory stock. All work was done on first generation laboratory-raised animals. The animals were kept in a room with controlled temperature (20-27°C) and photoperiod 12L:12D. Animals were tested at about 22°C.

Training in preparation for the tests

There were three ways in which *A.antipodiana* were fed. These were to provide them with *Achaearanea* sp. spiderlings (hereafter referred to as 'spiderlings'), provide them with foodbundles, or to let them feed with the host. Feeding on spiderlings and feeding with the host provided *A.antipodiana* with training at araneophagy and kleptoparasitism, respectively.

Providing *A.antipodiana* with foodbundles

The 'foodbundle' was the easiest feeding option given to *A.antipodiana* as it would seem little or no hunting skills were required for it to obtain food in this way. All newly-hatched *A.antipodiana* were fed in this manner, as it was a very successful means of raising young

spiders to a size at which they could easily feed with the host or catch spiderlings.

To provide *A.antipodiana* with foodbundles, adult *Achaearanea* sp. were housed individually in small cylindrical cages (6 cm tall, 5 cm diameter) and fed fruitflies. *Achaearanea* sp. caught the flies by wrapping and then biting them. Each wrapped fruitfly was then hung in the web individually or in small groups. Once they were caught and wrapped, the fruitflies were called 'foodbundles'. After an *Achaearanea* sp. had caught some fruitflies and begun feeding, it was removed from the cage while the foodbundles were left intact. *A.antipodiana* was then added to the cage and allowed to feed on the foodbundles. Each week, *A.antipodiana* was moved to a fresh cage containing foodbundles.

Training *A.antipodiana* to feed araneophagically (catch spiderlings)

To train *A.antipodiana* to catch spiderlings, *A.antipodiana* was housed in small cylindrical cages and were provided with about 20 spiderlings and about 8 fruitflies per week. *A.antipodiana* was then left to catch the spiderlings and fruitflies.

The fruitflies were added to provide *A.antipodiana* with an extra food source. The rationale for doing this was as follows: if *A.antipodiana* was only fed spiderlings, then the only way that it could feed would have been through catching spiderlings. If it was unable to feed in this manner, it may have died. Consequently, any difference in spiderling-capturing abilities between the trained and untrained group may not be because *A.antipodiana* had improved its ability at capturing spiderlings, but, instead, because of selective mortality; that is, *A.antipodiana* that were innately better at catching spiderlings might be more likely to survive. Because I supplemented spiderlings with fruitflies, selective mortality of this kind should not have biased results.

Training *A. antipodiana* to feed kleptoparasitically

Initially, each *Eriophora pustulosa* (the primary host of *A. antipodiana* in the field) was housed in a large plastic cage (either 200x60x200 mm or 100x60x150 mm) and allowed to build vertical orb web. *A. antipodiana* was added to the cage and allowed to build its web attached to that of the host. Next, houseflies and fruitflies were added once a week.

The houseflies were added in order to train *A. antipodiana* to feed with the host. Houseflies are very difficult for *A. antipodiana* to catch on their own (pers. obs.). Thus virtually the only way that *A. antipodiana* could feed on the houseflies provided would be to kleptoparasitize those that the host had caught (either by feeding with the host or stealing the wrapped up housefly).

As in the previous training regime, fruitflies provided *A. antipodiana* with another source of food. Thus *A. antipodiana* could glean the fruitflies off the web without needing to interact directly with the host. If only houseflies were provided, then the only way that *A. antipodiana* could feed would have been through interacting with the host. If it was unable to feed in this manner, it may have died. Consequently, any difference in the kleptoparasitic behaviour of trained and untrained *A. antipodiana* may have simply reflected selective mortality. I supplemented the housefly-fed *A. antipodiana* with fruitflies so that selective mortality of this kind should not bias results.

Testing

When an animal was two moults away from maturity, it was put into its first feeding training programme and tested when it matured. As the lifespan of *A. antipodiana* can vary greatly (for example, individuals can take between 1 and 9 months to mature; unpubl. data), each of the 149 *A. antipodiana* used in these experiments had to be followed individually to

ensure that they were put into a training programme and removed from the training programme at the right stage (see later) of their development. Even though the training programme for each *A. antipodiana* was dictated by its own development, each *A. antipodiana* spent at least 30 days in its training programme.

SECTION ONE: FEEDING ARANEOPHAGICALLY

METHODS

Training protocol

Four different training protocols were adopted to obtain *A. antipodiana* with different degrees of experience at feeding araneophagically on *Achaearanea* sp. spiderlings (Fig. 1). After a training protocol had been completed, the *A. antipodiana* was tested to gauge its ability to capture spiderlings.

In preparation for test 1.1 spiders were trained araneophagically (i.e. trained to catch spiderlings) from two moults before maturity (body length 0.87-1.30 mm) and until they were tested, which was within the first three weeks of maturing. For test 1.2 spiders were trained kleptoparasitically (that is, trained to feed with the host) from two moults before maturity and were then tested within the first three weeks of maturing. The spiders used in test 1.2 were then trained araneophagically. This was done in order to determine whether *A. antipodiana* improved their ability to capture spiderlings (i.e. feed araneophagically) after maturing (test 1.3). The spiders used in test 1.4 were simply fed food bundles until they were sub-adult (i.e. in their penultimate instar), at which point they were tested to see if they could capture spiderlings.

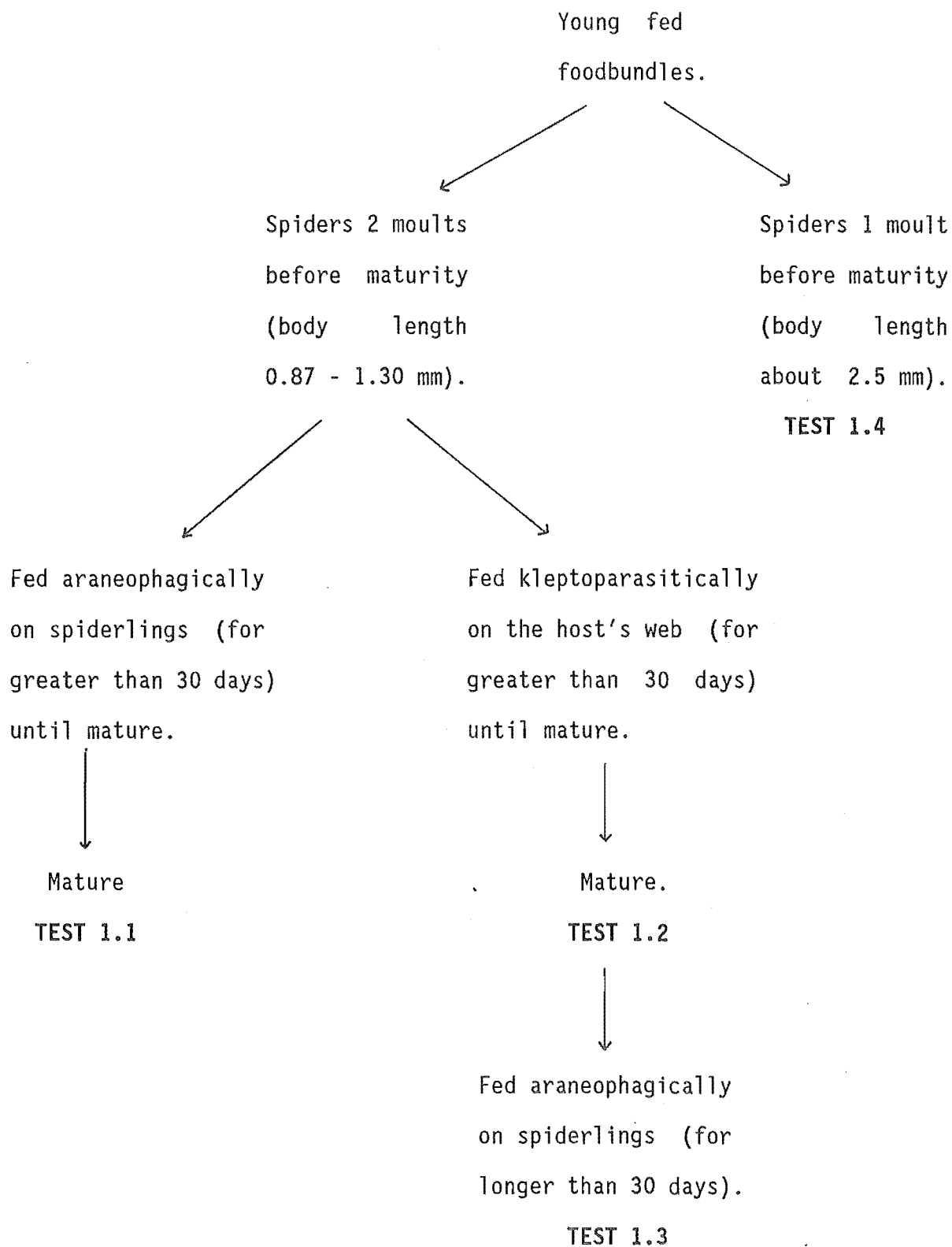


Fig. 1. Tests conducted on *A. antipodiana* to determine whether they improve their ability to capture spiderlings.

Comparing Tests

By comparing the results of the four tests, it was possible to ask four questions on the nature of *A. antipodiana*'s ability to feed araneophagically.

Are *A. antipodiana* able to improve their ability to capture spiderlings as juveniles?

By comparing test 1.1 with test 1.2, it is possible to see if adult *A. antipodiana* which have had experience at capturing spiderlings when they were juveniles are better at capturing spiderlings than adult *A. antipodiana* which have not had this experience.

Is improvement in ability to capture spiderlings determined by developmental changes rather than learning?

Learning is not the only means by which an animal can improve its ability to perform an action. Other factors, such as developmental changes (maturation), may enable an animal to improve its ability at a specified task. For example, *A. antipodiana* might simply get better at predation on spiderlings as it gets older without experience with prey having any effect.

To determine whether there is any evidence of this, *A. antipodiana* which had had experience at capturing spiderlings only after they had become adults (test 1.3) were compared with *A. antipodiana* which had had experience at capturing only when they were juveniles (test 1.1; Fig. 1). If spiders in test 1.3 did better than those in test 1.1, then it would seem that ability to capture spiderlings simply improved with age and would signify a developmental change in behaviour rather than a behavioural change caused by experience.

Is *A. antipodiana* able to improve its ability to capture spiderlings after it has become an adult?

By comparing the results of test 1.2 with test 1.3, it is possible to establish whether those *A. antipodiana* that had no experience of capturing spiderlings as juveniles could improve their ability to capture spiderlings if they can gain experience of capturing spiderlings as adults.

Does *A. antipodiana*'s ability to catch spiderlings deteriorate?

Besides being acquired, behaviour can be lost. For example, it is conceivable that an animal may initially be able to perform a behaviour but, if it does not do so within a critical period, it will lose that ability.

It is possible that *A. antipodiana* may be initially good at catching spiderlings, but if it is not exposed to spiderlings as a juvenile, then it may lose this ability. To ascertain whether *A. antipodiana* are initially able to catch spiderlings or not, a comparison was made between the results of test 1.4 and test 1.2. to see if inexperienced sub-adults and inexperienced adults differed in their ability to catch spiderlings.

Testing Procedure

A. antipodiana were placed in clean small cylindrical containers (described above) and left to adjust for at least a day. To test the ability of *A. antipodiana* to capture spiderlings, 14-20 *Achaearanea* spiderlings (c. 0.8mm long) were added to the cage and *A. antipodiana* was then observed continuously for 1 h. After this period, the spiderlings were removed. This testing procedure was repeated 6 times within a 10-day period. No spider was tested more than once per day. If a spider attempted to capture fewer than 10 spiderlings in the 6 hs of observation, its results were discarded from the analysis.

Sometimes 6 h tests could not be completed. This was particularly a problem with sub-adult spiders which sometimes matured during the 10-day testing period. These results, though, are still included in this analysis (as long as the *A.antipodiana* attempted to capture more than 10 spiderlings).

Data on the ability of *A.antipodiana* to capture spiderlings during the 1 h long tests were gathered in two forms. First, an attempt to establish prey capture efficiency was made. To do this, all attempts by the *A.antipodiana* to capture prey were recorded. (Definition: a spider 'tried' to capture a spiderling if it lunged at the spiderling or began to wrap it up). Prey-capture efficiency was calculated by dividing the number of spiderlings caught by the total number of attempts (expressed as a percentage). Second, records of the prey capture sequences were recorded to see if improved capture efficiency was reflected in a change in details of behaviour.

Because *A.antipodiana* were followed individually and tested when their particular training programme was completed, spiders from any of the training programmes (1.1, 1.2, 1.3, 1.4) were ready for testing on any particular day. Subsequently, the observer did not know which training programme had been used on any particular test spider, enabling the tests to be conducted 'blind'.

Terminology

Spiders full lunged (described in detail elsewhere: Whitehouse 1986) by extending their legs I and II forward in unison towards the prey, then scooping in the prey towards its mouth by using tarsi of legs I and II. If *A.antipodiana* missed the prey, the action was the same. *A.antipodiana* bit the prey if, at the end of the lunge, *A.antipodiana's* chelicerae made contact with the prey. A half lunge was similar to the full lunge except that it was incomplete; this was because the spider's tarsi moved only

about half way to the mouth. A scrabble lunge was also similar to a full lunge except the legs I and II did not move in unison. Nevertheless, the tarsi of each leg still completed its movement to the mouth of *A.antipodiana*. During a scrabble lunge, the body of *A.antipodiana* rocked forward. Scrabbles differed from scrabble lunges in that the legs I and II again extended forward and the tarsi was pulled back towards the mouth; but this time the movements were of much smaller amplitude, performed randomly, and the spider's tarsi did not reach the mouth. *A.antipodiana* tensed by stiffening its legs. Wrapping (described in detail elsewhere: Whitehouse 1986) involved *A.antipodiana* throwing silk over the prey, or in the direction of the prey, with its legs IV. It did this by facing away from the prey and drawing out silk from its spinnerets with its legs IV, moving in alternating phase. To fast grab, (described in detail elsewhere: Whitehouse in prep.) one spider pulled rapidly with its legs I and II on the dragline of the other spider, as if it was trying to haul in the other spider. Body shuddering (described in detail elsewhere: Whitehouse in prep.) involved *A.antipodiana* vibrating its abdomen rapidly in 1 s bursts. A violent shudder (described in detail elsewhere: see Whitehouse in prep.) involved the spider flexing its legs so that it performed a large amplitude (c. 2mm) oscillation on the web. To touch another spider, *A.antipodiana* extended a leg I and brought its tarsus into contact with the other spider.

RESULTS

Over all, 86 spiders were observed for 699 hrs in 121 tests. To catch spiderlings, *A.antipodiana* characteristically moved slowly towards the spiderling until it was about 1-2 mm in front of the spiderling. At this point, *A.antipodiana* paused, then lunged at the spiderling, pulling it in towards its mouth where it was bitten. After biting the spiderling, *A.antipodiana* slowly wrapped it.

As males and females may differ in their ability to capture spiderlings, results were analysed with the sexes both combined and separated.

Preliminary tests

Preliminary work revealed that *A.antipodiana* were too small to test with *Achaearanea* when two moults before maturity (out of the 9 animals tested, only 3 animals tried to capture the spiderlings within 54 hrs of observations, 2 of these lunged once, and 1 lunged three times and caught 1 spiderling). However, sub-adult *A.antipodiana* (one moult before maturity) were large enough to test.

Comparing tests

Do *A.antipodiana* learn to capture spiderlings as juveniles?

All the following analysis was based on Mann-Whitney U tests. Adult *A.antipodiana* which had been trained to feed araneophagically as juveniles (test 1.1) had a greater araneophagic prey-capture efficiency than those (test 1.2) that had not ($P=0.009$; $n=40$). However, results for males differed from results for females (Fig. 2). Trained (experienced) males were more efficient than untrained (inexperienced) males at capturing spiderlings ($P=0.014$, $n=21$) while there was no evidence of a similar difference between experienced and inexperienced females ($P=0.24$, NS, $n=19$). Thus males and females appeared to differ in their responsiveness to training.

However, when prey-capture efficiency of males and females are compared directly, there is no significant difference (experienced males compared to experienced females, $P=0.57$, NS, $n=21$; untrained males compared to untrained females, $P=0.06$, NS, $n=21$). There does, nevertheless, seem to be a tendency for untrained female *A.antipodiana* to be better at catching spiderlings than untrained males ($P=0.06$, NS, $n=21$).

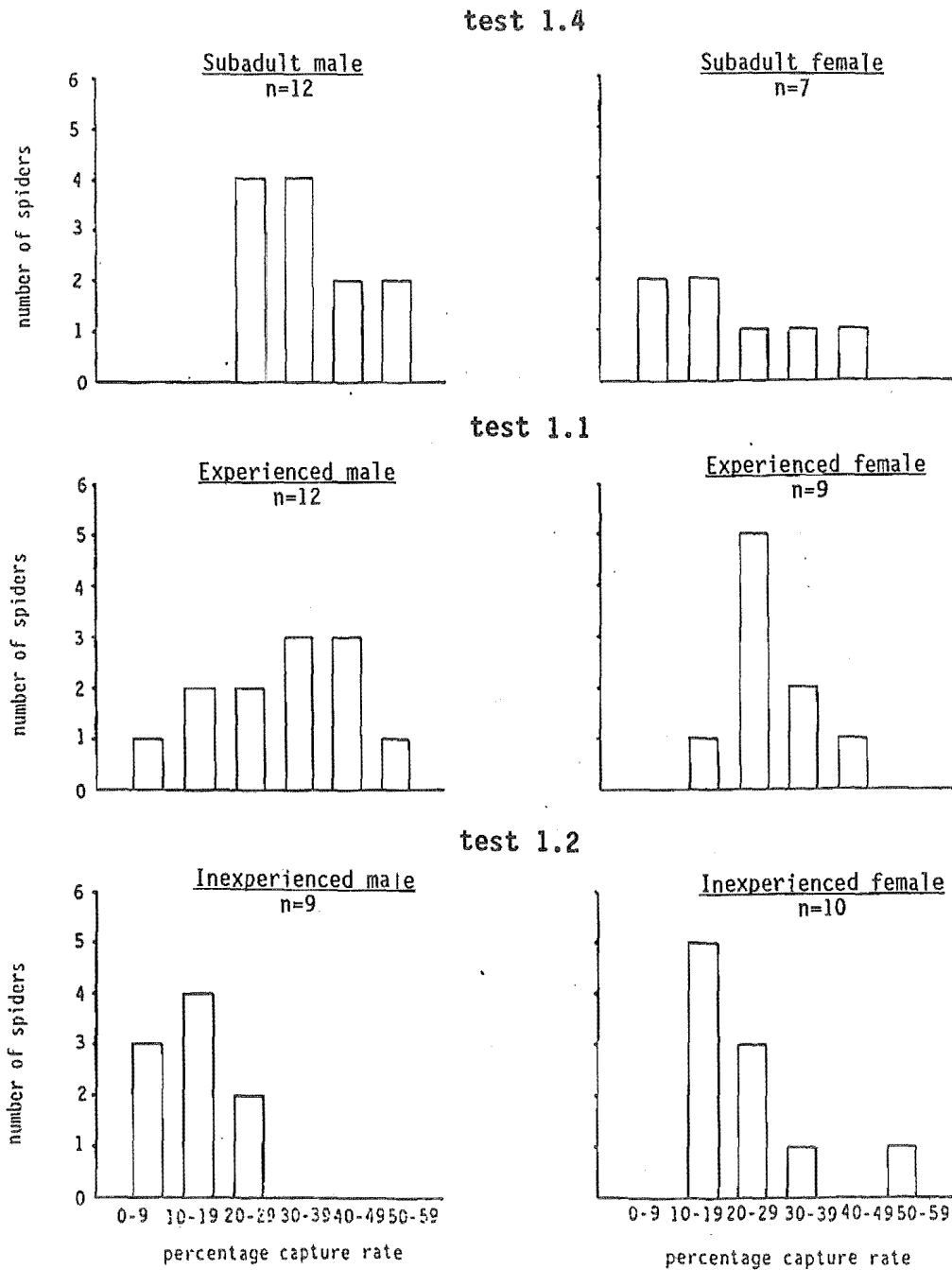


Fig. 2. Histograms of the percentage prey-capture rate of the spiders in tests 1.1 and 1.2. Percentage prey-capture rate was calculated by dividing the number of successful prey-capture attempts by the total number of attempts and multiplying by 100.

Prey-capture techniques

Prey-capture techniques were analysed to see if the difference in prey capture efficiency could be accounted for by details of *A. antipodiana*'s predatory behaviour. Both sexes usually caught spiderlings by lunging (94% of 252 catches). However, although there was no evidence that experience influenced behavioural differences between the sexes, males and females in tests 1.1 and 1.2 differed in their tendency to use minor techniques to try to capture spiderlings:

Scrabble lunge: Twenty out of 21 males scrabbled lunged whereas only 12 out of 19 females scrabbled lunged at spiderlings (test of independence: $\chi^2=7.98$, $P<0.005$, $n=40$). Thus males were more likely to scrabble-lunge than females.

Wrapping: Twelve out of 19 females tried to capture spiderlings by wrapping whereas only 2 out of 21 males attempted this technique. Thus females were more likely to try and capture spiderlings by wrapping than males (test of independence: $\chi^2=12.61$, $P<0.0005$, $n=40$).

Dropping: After successfully lunging and catching prey, *A. antipodiana* often dropped the prey when trying to wrap it. However, there was no difference between males and females dropping prey as 13 females out of 19 dropped prey while 16 males out of 21 dropped prey (test of independence: $\chi^2=0.03$, NS, $n=40$). Neither was there any evidence that experienced spiders differed from inexperienced spiders in how often they dropped prey. Seventeen out of 21 experienced spiders dropped prey whereas 12 out of 19 inexperienced dropped prey (test of independence: $\chi^2=1.58$, NS, $n=40$).

Mistakes: Often *A. antipodiana* were observed lunging in the wrong direction from a prey item, or apparently misjudged the distance to the prey item when they lunged, or lunged at the prey item after it had already dropped to safety. Twelve out of 21 experienced spiders made these mistakes compared to 17 out of 19 inexperienced spiders. (test of

independence: $\chi^2=5.23$, $P=0.02$, $n=40$). Thus experienced *A. antipodiana* were less likely to make mistakes than inexperienced *A. antipodiana*. All 10 inexperienced females made mistakes, 7 of the 8 inexperienced males made mistakes, 6 of the 9 experienced females made mistakes, while 6 of the 12 experienced males made mistakes.

Touch: Sometimes *A. antipodiana* touched the prey before lunging. There was an interesting trend here: experienced females appear more likely to touch the prey than inexperienced females (although the trend is not significant in a chi-square test of independence: $P=0.07$, NS, $n=19$) as 8 out of 9 experienced females touched compared to 5 out of 10 inexperienced females. The opposite was true of the males as only 2 out of 10 experienced males touched compared to 6 out of 9 inexperienced males (test of independence: $P=0.02$, $n=21$).

Is improvement in ability to capture spiderlings determined by changes after maturity rather than learning?

The prey capture efficiency of *A. antipodiana* that had had experience at capturing spiderlings as juveniles (test 1.1) was compared with that of *A. antipodiana* that had had experience at capturing spiderlings only as adults (test 1.3). If the adults (test 1.3) were better at capturing spiderlings than the juveniles (test 1.1), then this may indicate that *A. antipodiana* improves its ability to capture spiderlings with age. However it was found that *A. antipodiana* with experience as adults (test 1.3) were actually worse at catching spiderlings than *A. antipodiana* with experience as juveniles (test 1.1), (Mann-Whitney U test: $P=0.01$, $n=30$). Thus prey-capture efficiency does not improve developmentally with increasing age.

Are *A. antipodiana* able to improve their ability to capture spiderlings after they become adults?

Nine spiders (3 males and 6 females) completed both tests 1.2 and 1.3 satisfactory. Four of these (2 males and 2 females) increased their prey capture efficiency in test 1.3 but five (1 male and 4 females) did not. Therefore, there is no clear evidence that adult experience improves ability to capture spiderlings.

Does *A. antipodiana*'s ability to capture spiderlings deteriorate?

Over all, inexperienced sub-adults (test 1.4) were no better than inexperienced adults (test 1.2) at capturing spiderlings (Mann-Whitney U test: $P=0.33$, NS, $n=38$). However, if the sexes are analysed separately, it becomes apparent that this is not the complete picture. Although sub-adult females do not differ from adult females in their ability to capture spiderlings (Mann-Whitney U test: $P=0.35$, NS, $n=17$), sub-adult males are considerably better than adult males at capturing spiderlings ($P=0.0002$, $n=21$). Additionally, sub-adult males were significantly better at catching spiderlings than sub-adult females (Mann-Whitney U test: $P=0.02$, $n=19$). Consequently, it appears that if males are never exposed to spiderlings, they are initially good at capturing spiderlings as sub-adults, but become poor at capturing spiderlings once they mature.

An artifact which could have accounted for this difference must be considered: perhaps adult male spiders are simply not as interested as females in capturing spiderlings. This does not appear to be so. I compared the number of prey-capture attempts by adult versus sub-adult males. There was no evidence that they differed (Mann-Whitney U test: $P=0.62$, NS, $n=21$).

DISCUSSION

Behavioural differences between males and females

Results from this study indicate that *A. antipodiana* can improve its ability to capture spiderlings if it is exposed to them as a juvenile. However, this improvement appears to occur only in males. Although inexperienced adult females tended to be better than inexperienced adult males at catching spiderlings, they were also as good as experienced adult females at catching spiderlings. In contrast, experienced adult males were much better than inexperienced adult males at catching spiderlings.

Thus males appeared to improve their ability to capture spiderlings with experience, while females did not. However, the story is more complex than this. Although sub-adult females were poor at catching spiderlings, sub-adult males with no previous experience excelled at catching spiderlings. Thus experienced males appeared to be good at catching spiderlings because they retained the ability they had as sub-adults, rather than because they developed this ability through practice. Inexperienced *A. antipodiana* which did not capture spiderlings as juveniles appeared to lose this ability.

Behaviours used in araneophagy

Behavioural differences between the sexes.

The differences between the abilities of males and females to capture spiderlings is reflected in behavioural differences between the sexes. Although both sexes attempted to catch spiderlings primarily by lunging, males were more likely to try to scabble-lunge at spiderlings, while females were more likely to try to wrap them up. These differences in how males and females attempted to catch spiderlings were not related to experience and seemed to be inherent differences between males and females. Experience did, though, tend to make females more prone to touch prey before lunging, but paradoxically, experience appeared to make males

less prone to touch prey before lunging. The reason for this difference is unclear.

Behavioural differences between experienced and inexperienced araneophagic *A. antipodiana*.

Other behavioural observations revealed important behavioural differences between experienced and inexperienced *A. antipodiana*. To capture spiderlings, *A. antipodiana* first must lunge accurately at the prey. Secondly it must retain a hold upon the prey while biting the prey and then wrap up the prey. Experienced and inexperienced spiders appeared to be equally likely to make mistakes at the second step in that they were equally likely to drop prey after capturing it. The only behaviour in which experienced spiders were significantly better than inexperienced spiders was lunging.

This is intriguing as it indicated that to improve prey-capture ability *A. antipodiana* did not need to improve their general ability to capture spiderlings, but only a part of their prey-capture sequence (lunging).

Is there a critical period for the acquisition of araneophagy?

It appears that adult males with experience were better than adult males without experience at catching spiderlings because the experienced males retained the ability to capture spiderlings which they had as sub-adults. As the ability of *A. antipodiana* to capture spiderlings appeared to deteriorate if not practised, and as only a small part of the prey capture sequence was affected, it is possible that araneophagic skills may be controlled by a critical period, specifically related to lunging accuracy.

Critical periods are short time spans in an animal's history when it is particularly sensitive to a specific stimulus. Exposure to that

stimulus at that time affects the animal's subsequent behaviour. For example, some song birds need to be exposed to their species specific song at a critical time in order to perform that song later as adults (Baptista and Petrinovich 1986). Additionally, a critical period is important in the development of vision in cats (Aoki and Siekevitz 1988). Cats are born with the neurons in the neuron networks of both eyes intact and each of these neuron networks have many connections or potential connections, but only the connections which are used during a critical period of 2-4 months get "fixed". If one eye is covered and the other exposed to light, only the connections in the exposed eye are being used, and thus only these develop micro-tubule skeletons which are necessary for dendritic connections to both develop and become fixed. Thus the neuron network of the deprived eye does not develop and the eye is effectively blind, even if it is later exposed to light.

The process by which lunging in *A.antipodiana* is retained may be in principle similar to the way in which cat vision develops. For instance, different feeding behaviours including lunging may be completely encoded from birth in the neuron networks. If the spider does not use lunging during the critical period, the neural network that encodes lunging accuracy may deteriorate, rendering the animal less capable of lunging as an adult.

If lunging accuracy is controlled by a critical period, it would explain why inexperienced sub-adult males were so good at lunging, why some experienced adult males were as good as the sub-adults at lunging, and why inexperienced adult males were so poor at lunging. One could also predict (if this is correct) that *A.antipodiana* would not be able to improve lunging behaviours as adults. This prediction is in agreement with the preliminary results where adult *A.antipodiana* appeared unable to improve their ability to capture spiderlings after exposure to spiderlings as adults.

So even though experienced spiders were better than inexperienced spiders at catching spiderlings, the difference does not appear to be the result of learning by trial and error, but apparently due to the maintenance of a behaviour usually lost. By using a critical period in this manner, *A. antipodiana* is able to discard lunging accuracy if it is not going to be useful (i.e. if there are no spiderlings around to catch), but maintain it if it will be useful. However, it is unclear why it would be advantageous to lose the technique - unless it was energetically expensive. Nevertheless, this technique apparently affords a lot of flexibility to the feeding behavioural repertoire of *A. antipodiana* without requiring *A. antipodiana* to develop advanced cognitive skills.

SECTION TWO: FEEDING WITH THE HOST

METHODS

Training protocol

Four training protocols were used to see whether *A. antipodiana* could, with practice, improve its ability to feed kleptoparasitically (Fig. 3). In preparation for test 2.1, spiders were trained kleptoparasitically from 2 moults before maturity until they were tested, which was within the first 3 weeks of maturing. For test 2.2, spiders were trained araneophagically from 2 moults before maturity and were then tested within the first 3 weeks of maturing. The spiders used in test 2.2 were then trained kleptoparasitically as adults (test 2.4). The spiders used in test 2.1 were, as adults, fed on spiderlings and fruitflies for at least 22 days to see if their ability to feed with the host deteriorated (test 2.3).

Comparing tests

Tests 2.1 and 2.2 were compared to see if *A. antipodiana* which had experience at feeding with the host as juveniles were better at

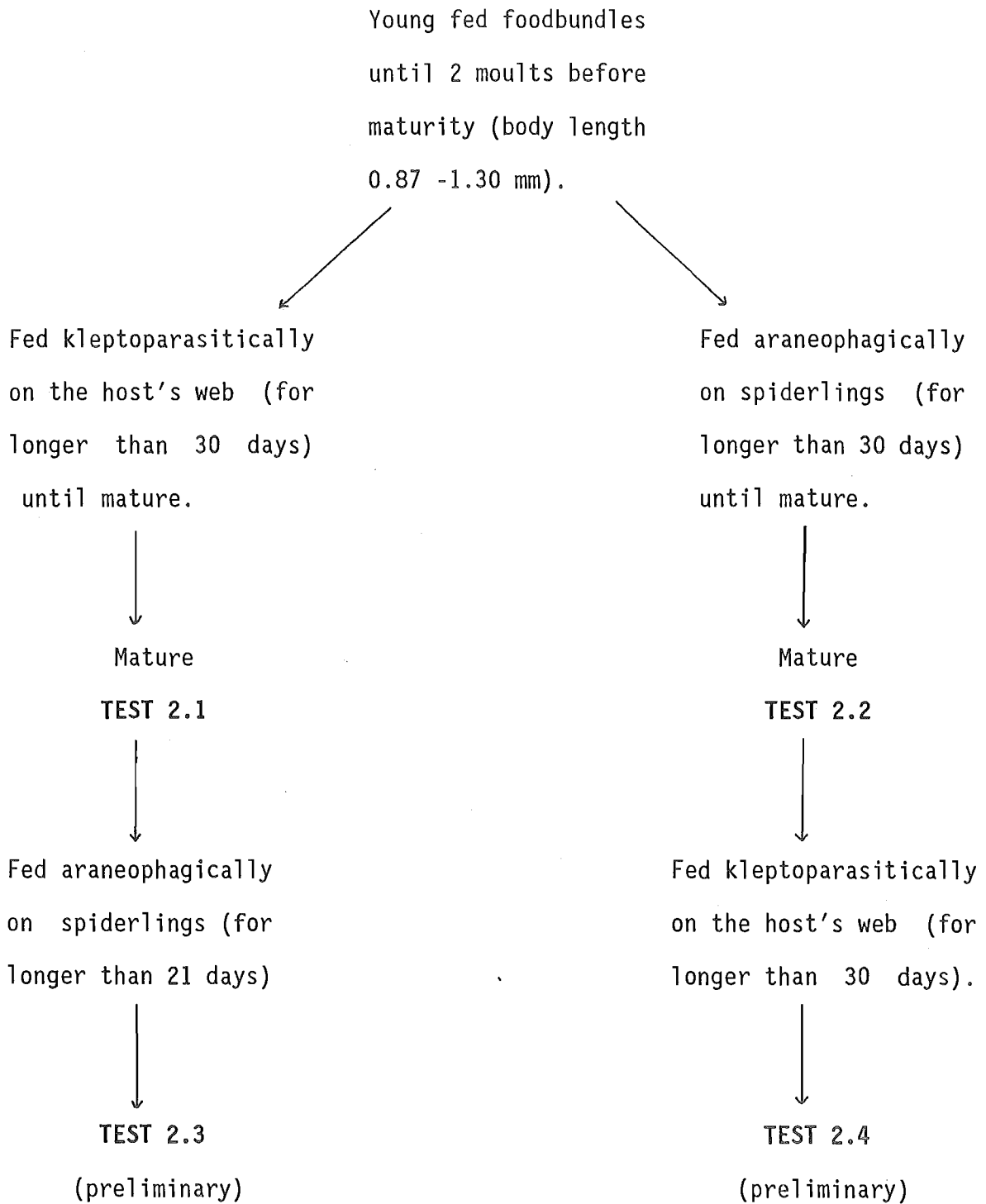


Fig. 3. The testing procedure to establish if *A. antipodiana* improves its ability to kleptoparasitize the host. The tests examined *A. antipodiana*'s ability at feeding with the host.

kleptoparasitism than *A.antipodiana* which had not had experience at feeding with the host as juveniles.

Tests 2.1 and 2.3 were compared to see whether kleptoparasitic abilities acquired as juveniles deteriorated in the adult *A.antipodiana* if it was no longer feeding kleptoparasitically.

Tests 2.2 and 2.4 were compared to see whether *A.antipodiana* which had had no kleptoparasitic experience as juveniles could improve kleptoparasitic abilities if they were trained kleptoparasitically as adults.

Background information on feeding behaviour

Feeding with the host is the main means by which *A.antipodiana* feeds on large prey items caught by the host. The normal procedure involves the host, which is already positioned at the hub, running over to a struggling food item, biting it and then wrapping it before carrying it back to the hub to feed (Fig. 4). *A.antipodiana* responds to these vibrations by moving down the radii of the web towards the hub so that it too can feed on the food bundle the host is consuming (see Whitehouse 1986 for a more detailed explanation of the foraging behaviours of *A.antipodiana*).

To feed with the host *A.antipodiana* has to cope with a number of problems. Initially it has to realize that the host has caught prey and is vulnerable to kleptoparasitism; then it had to locate the host and food. The host normally feeds at the centre of the web, so the easiest approach is to go down a radius. Once *A.antipodiana* has located the host and food, it may still be unable to feed. *A.antipodiana* may either have to approach again from a different angle to reach the food or have to go around to the other side of the web to reach the food, or may have to reach through the plane of the web to arrive at the food.

The best way for *A.antipodiana* to feed with the host *Eriophora pustulosa* (Fig. 5) is to position itself on the side of the web opposite

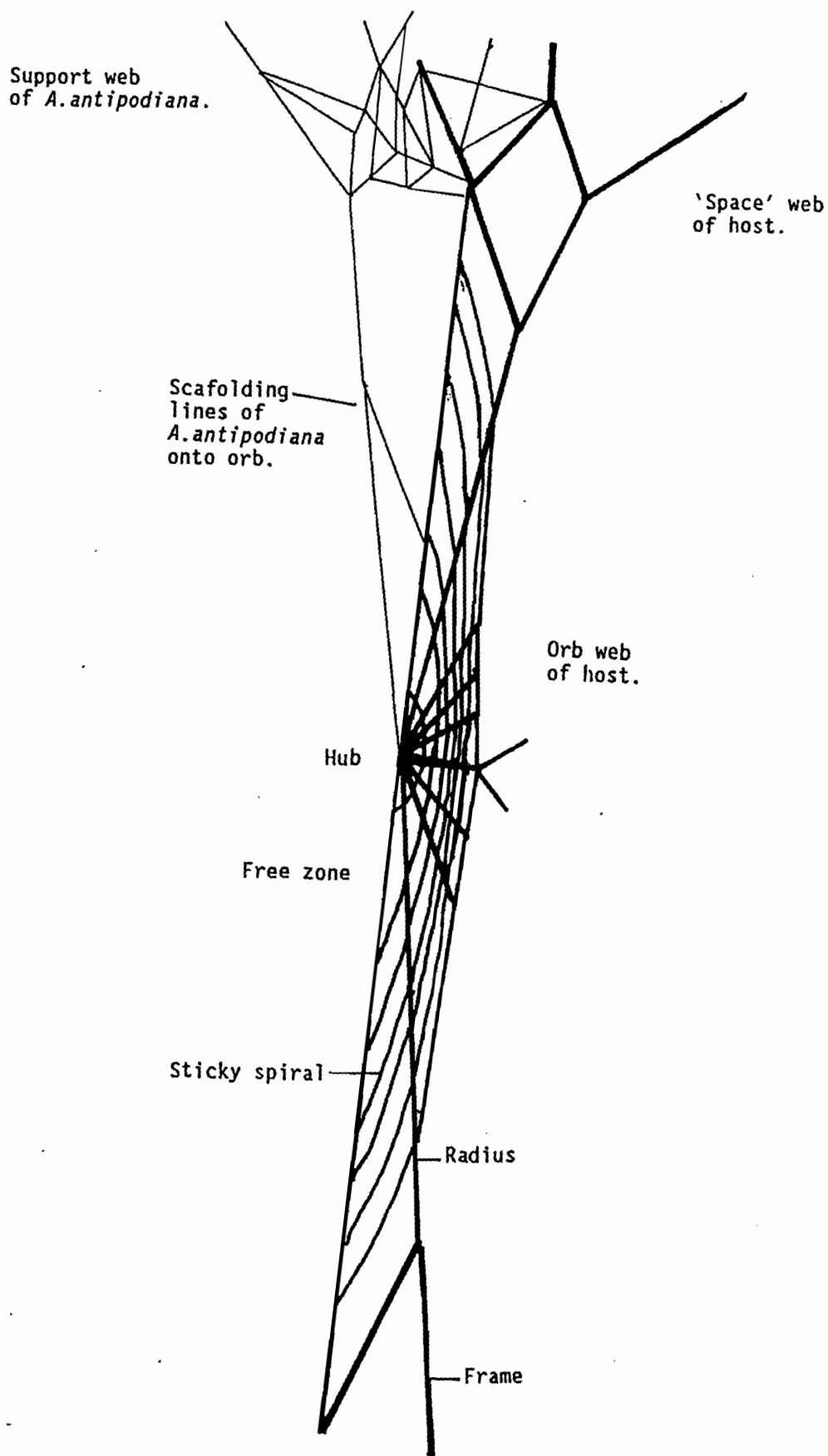


Fig. 4. The web complex, which includes the support web of *A. antipodiana* and the orb web of the host, *E. pustulosa*.

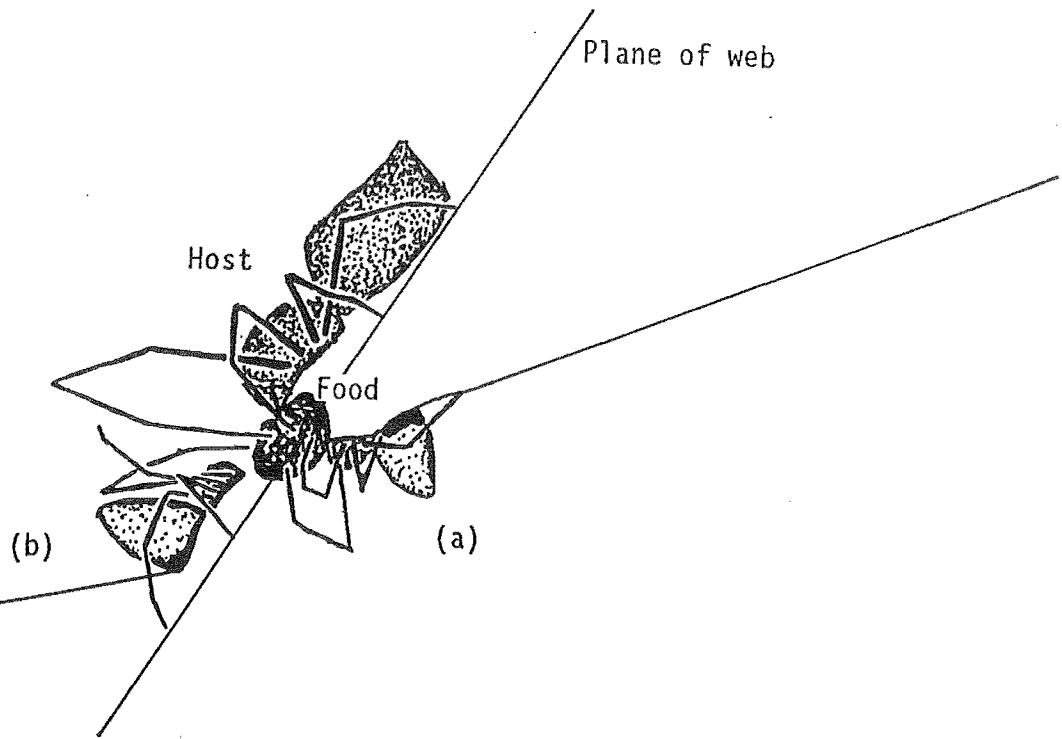


Fig. 5. Relative positions of host and *A. antipodiana* when feeding with host. (a) 'better' position for *A. antipodiana*. Food is easily reached and the plane of the web is between *A. antipodiana* and the host. (b) Riskier feeding position. The host can easily reach *A. antipodiana* while *A. antipodiana* has difficulty reaching the food.

the host. By feeding on the side of the web opposite the host, *A.antipodiana* can gain access to all sizes of food items including small items, upon which the host may be feeding. Additionally, feeding on this side means that the plane of the web, which is between *A.antipodiana* and the host, acts as a barrier between the host and *A.antipodiana*. Thus feeding from the opposite side of the web may be safer than feeding from the same side of the web as the host. If *A.antipodiana* reaches the hub but finds it is on the same side of the web as the host, it usually goes back to the edge of the web and approaches again on the opposite side before feeding. However, occasionally the foodbundle is large enough that *A.antipodiana* can feed safely on the same side of the web as the host.

A.antipodiana does not always need to move back to the edge of the web before moving from the same to the opposite side; instead, *A.antipodiana* may slip through spaces in the web near the hub, or the host itself may move around to the other side of the web, leaving *A.antipodiana* on the opposite side.

There are other ways in which *A.antipodiana* can forage kleptoparasitically in the host's web. It can physically remove foodbundles the host leaves unguarded (i.e., "steal" foodbundles) and hoist them into its own web. Alternatively, it can simply catch small flies caught on the host's web that the host has ignored.

Testing procedure

Eriophora pustulosa was set up in clear plastic cages (10x15x6 cm) about one week before the test and allowed to establish orb webs. An *A.antipodiana* was then added to the cage and left for about 5 mins to allow it to locate the web and orient itself. Once *A.antipodiana* had positioned itself on the side of the web, two houseflies were added to the cage. If the host did not catch either fly, the test was aborted. If the host finished eating the two available flies before the test was

completed, more flies were added. Out of the 186 tests conducted, only the tests where *A.antipodiana* attempted to feed with the host (n=110) were analysed. This was to try to reduce a possible bias caused by hunger.

If *A.antipodiana* responds to the host catching prey, then presumably it is hungry. If *A.antipodiana* does not respond, then it may simply not be hungry. Responding to the host indicated a certain degree of hunger and by using these tests only, I was able to compare the abilities of *A.antipodiana* to feed with the host rather than compare their hunger level.

The test was ignored if *A.antipodiana* stole a foodbundle, fed upon a foodbundle upon which the host was not feeding, or caught its own fly. Likewise, if the host fed at the side of the web instead of at the centre, the test was ignored.

Analysis

Does *A.antipodiana* respond kleptoparasitically to prey capture by the host?

A.antipodiana was allowed 50 min to reach the hub from the time the host caught the fly. If it reached the hub within this 50 min, it was recorded as 'responding kleptoparasitically'.

Does *A.antipodiana* feed with the host once it reaches the hub?

A maximum period of 50 min from the first approach towards the hub by *A.antipodiana* was allowed for feeding with the host to begin.

Does training affect the speed at which *A.antipodiana* obtains food?

For this, I recorded the time it took *A.antipodiana* to obtain food, once it had started approaching the hub. I compared the results obtained from the different tests to see if there were any changes in the time it took *A.antipodiana* to obtain food. Only those *A.antipodiana* that fed

within the allotted time period were used in this analysis.

How well does *A.antipodiana* respond to problems encountered when trying to feed with the host?

In particular, I examined how *A.antipodiana* coped with the problems of reaching the hub on the 'wrong' side, a problem that could be corrected by approaching the hub again from the other side. The number of times *A.antipodiana* made this adjustment was recorded, then the test results were compared.

RESULTS

As males and females responded differently in the tests, results from tests of males and females are analysed separately.

Effects of training on the ability of juveniles to feed with the host

Does *A.antipodiana* respond kleptoparasitically to prey capture by the host?

Twenty three of the 24 trained males (test 2.1) that tried to reach the hub did so while only 19 of the 27 untrained males (test 2.2) reached the hub. Thus males that had been trained as kleptoparasites while juveniles were more likely to respond to prey catching by the host and reach the hub than males that had not been trained as kleptoparasites as juveniles (test of independence: $\chi^2=4.059$, $P<0.05$, $n=51$). However, 16 of the 20 trained females (test 2.1) that tried to reach the hub did so while 9 of the 12 untrained females (test 2.2) did likewise. Thus females that had been trained as kleptoparasites while juvenile appeared to be no more likely to feed with the host than untrained females (test of independence: $\chi^2=0.09$, NS, $n=32$).

Does *A. antipodiana* feed with the host once it reaches the hub?

Of the 23 trained males that reached the hub, 19 fed while of the 19 untrained males that reached the hub, 14 fed. Thus untrained males (test 2.2) that reached the hub were just as likely as trained males (test 2.1) that reached the hub to feed with the host in 50 mins (test of independence: $\chi^2=0.10$, NS, $n=42$). The same was true of trained (test 2.1) and untrained (test 2.2) females. Only one untrained female out of all the 29 females tested (13 untrained and 16 trained) did not feed with the host in the allotted time.

Does training affect the speed at which *A. antipodiana* obtains food?

Although it appeared that there was a tendency for trained males to reach the hub faster than untrained males (Mann-Whitney U test: $P=0.056$, NS, $n=23$), there was no suggestion of trained females reaching the hub faster than untrained females (Mann-Whitney U test: $P=0.12$, NS, $n=15$).

How well does *A. antipodiana* respond to problems encountered when trying to feed with the host?

To answer this question I looked at the ability of trained and untrained kleptoparasites to "move around" to the correct side of the orb web, after they initially approached the host from the "wrong" side. I compared trained males (test 2.2, Table 1) with untrained males (test 2.2, Table 1) by ignoring all instances in which the host moved to the other side (column 3, Table 1) and where *A. antipodiana* moved backward and forwards between the two sides (column 2, Table 1). I found that trained males were more likely to move around to the other side of the web than untrained males (test of independence using results in columns 1 and 4: $\chi^2=8.6$, $P<0.005$, $n=19$).

Untrained males that did not change sides still attempted to feed with the host by approaching the host from different angles.

Table 1. A list of the number of approaches that spiders made to the host if it initially approached from the wrong side. The table reveals that spiders with experience as either juveniles or adults (Tests 2.1 and 2.4) appear more likely to change sides than inexperienced spiders (Test 2.2). There was not enough data gathered from Test 2.3 for comparisons with this group to be made.

Number of attempts.				
	Before changing sides	Alternating between the two sides	Before the host changed sides	Did not change sides
Females with training as juveniles. Test 2.1. (n=6)	1 1 2 2 2			
		4		
Males with training as juveniles. Test 2.1 (n=11)	1 1 1 2 2 3 3 4 4 5			
		4		
Females with training as adults only. Test 2.4 (n=4)	1 1 1			3
Males with training as adults only. Test 2.4 (n=3)	2 5		2	
Untrained females. Test 2.2 (n=4)	4		3 4 5	
Untrained males. Test 2.2 (n=8)	1 4			2 3 3 4 4 5
Females forgetting. Test 2.3 (n=2)	1	1		
Males forgetting. Test 2.3 (n=3)	1	3		5

The ability of trained and untrained females to 'move around' could not be compared because the sample size for these tests was too small for statistical analysis (only 6 cases could be compared). For these 6 there was no clear trend (Table 1: untrained females test 2.2 and trained females test 2.1).

"Learning" as adults

Are *A. antipodiana* that gain kleptoparasitic experience only as adults (test 2.4, Fig. 3) more likely to feed with the host than untrained *A. antipodiana* (test 2.2, Fig. 3)?

Thirteen *A. antipodiana* tried to reach the hub as both untrained and then as trained adults. Of these, 1 did not feed on both occasions, 5 fed on both occasions, 3 fed as untrained adults only, and 4 fed as trained adults only. Subsequently, there was no evidence that *A. antipodiana* that gained experience solely as adults were more likely to feed with the host than untrained *A. antipodiana* (McNemar test for significance of change: $X^2=0.57$, NS, $n=13$, data of both sexes combined).

Nevertheless, *A. antipodiana* that had kleptoparasitic experience only as adults (test 2.4) seemed to be better at moving around to the correct side than inexperienced *A. antipodiana* (test 2.2). Of the 7 *A. antipodiana* with adult experience who approached the host on the wrong side 5 changed sides (Table 1, column 1, tests 2.4) while only 3 out of 12 inexperienced *A. antipodiana* (Table 1, column 1, tests 2.4) changed sides. However, this difference was not significant ($X^2=2.24$, NS, $n=19$).

"Forgetting" as adults

There was evidence that animals trained kleptoparasitically as juveniles were less likely to try to feed with the host after a period of feeding on spiderlings. Of the 11 *A. antipodiana* that tried to look for

food in both tests 2.1 and 2.3, 5 fed in both tests, and 6 fed in only the first test (2.1) before they were taken off the hosts web (McNemar test for significance of change: $\chi^2=4.16$, $P<0.05$, $n=11$, data from both sexes combined). Thus *A.antipodiana* were less likely to feed with the host if they had been away from a host's web for some time. There were insufficient data to compare the abilities of test 2.1 and 2.3 *A.antipodiana* to change sides as there were only 8 cases of test 2.3 animals attempting to feed from the wrong side. Of these, 2 changed sides, 1 did not, 1 went through the plane of the web to feed, and 2 alternated between the 2 sides (Table 1).

Do males differ from females in ability to change sides?

The number of attempts that males and females made before changing sides and approaching from the correct side were compared by pooling the results (Table 1, tests 2.1 and 2.4). Results indicate that there was a tendency for females to take fewer approaches to change sides than males (Mann-Whitney U test: $P=0.063$, NS, $n=20$).

DISCUSSION

Past experience apparently enabled *A.antipodiana* to solve problems associated with locating food at the hub. However, it did not apparently affect the spider's ability to behave kleptoparasitically. For instance, to gain access to food, both trained and untrained spiders were capable of firstly recognizing that the host had caught prey (i.e., they responded to the host catching prey); secondly, they both could respond appropriately to the host catching food (i.e., they moved down radii towards the hub), and thirdly, they could look for, find and feed on the foodbundle upon which the host was feeding.

The influence of familiarity on kleptoparasitism

All *A. antipodiana* were capable of kleptoparasitic behaviours. However they differed in their tendency to perform these behaviours, as some test groups appeared more likely to respond kleptoparasitically to the host catching food than others.

Consider this case. Untrained males were less likely to try to approach a feeding host than the other groups. This may indicate that males which have been living with *E. pustulosa* and are therefore more familiar with feeding kleptoparasitically, may be more motivated to feed kleptoparasitically than untrained males which have been feeding araneophagically. That is, familiarity may affect the tendency of *A. antipodiana* to feed with the host.

The effect of familiarity on food preference has often been reported in other invertebrates, such as the apple maggot fly, *Rhagoletis pomonella* (Papaj and Prokopy 1986), and the fruitfly, *Drosophila melanogaster* (Jaenike 1988). These animals are more likely to approach familiar food in order to feed or oviposit than approach unfamiliar food. Thus their tendency to respond to the different food-types is dependent on their exposure to the food-types.

This seems to be, in principle, similar to the response shown by male *A. antipodiana* when feeding kleptoparasitically. The animals tested here were either experienced or inexperienced in this feeding behaviour. When both groups of animals were given the option of feeding kleptoparasitically, males which had experience at feeding kleptoparasitically were more likely to respond to the food than males that had not - even though the inexperienced spiders were apparently just as capable of feeding kleptoparasitically as the experienced spiders.

This difference between trained and untrained animals was not, however, seen in the females. This may be because females in general are often more highly motivated to feed than males because females need to

increase their body size quickly and produce eggs. In contrast, males of some species of spiders may not feed at all (Bristowe 1958). Thus female *A. antipodiana* may be prepared to attempt to feed whenever possible, even by unfamiliar means.

Possible evidence of *A. antipodiana* solving problems

The major difference between trained and untrained spiders was their ability to develop solutions to novel problems when trying to feed with the host. The major problem associated with feeding with the host, *Eriophora pustulosa*, was locating the foodbundle. Usually, the best means of locating the foodbundle was to approach it from the side of the web opposite the host (Fig. 5). *A. antipodiana* that was experienced at kleptoparasitism (and especially if it was female) readily changed sides if it first approached the host and foodbundle from the 'wrong' side. Inexperienced *A. antipodiana*, however, did not. It usually continued to keep on trying to reach the food by staying on the same side of the web as the host. These results suggest that *A. antipodiana* may learn, through experience, that in order to feed with the host it is necessary to approach the host from the other side of the web. Thus *A. antipodiana* apparently learnt to solve the problem of locating the foodbundle.

Adults and juveniles appear to be more or less equally capable of solving problems associated with reaching foodbundles. That is, both adults and juveniles appeared to learn to change sides if they approached from the 'wrong' side. This suggests that developing solutions to feeding problems may not be restricted to a particular developmental period.

There is evidence that *A. antipodiana* may be able to solve other problems associated with feeding araneophagically. *A. antipodiana* occasionally encountered foodbundles that were too small to reach through the plane of the web. In order to feed off these foodbundles, *A. antipodiana* had either to reach through the plane of the web towards

them, or cut through some of the threads at the hub so that it could reach through to the foodbundle. Spiders from all test groups managed to solve the problem of reaching a small foodbundle, although there was not enough information to compare statistically the different groups' abilities at solving this problem.

Differences between males and females

As with lunging, there appears to be a difference between the abilities of the sexes to modify their kleptoparasitic behaviour. However, this time females were apparently better at learning than males. This difference in learning ability may reflect differences in motivation to feed.

For an animal to learn how to modify a behaviour, it must first be motivated to perform that behaviour. If an animal has little interest in performing a behaviour, it will not learn to perform that behaviour. Female *A. antipodiana* appeared to be better than males at solving problems associated with obtaining food.

Any differences between the males and females may explained by a difference in their motivation to feed. That is, females may be more inclined than males to try to reach the food even if doing so is difficult. Thus even though males and females were given the same amount of training time, females may have gained more 'practice' at reaching difficult foodbundles.

Another possibility is that females may simply be better at solving these problems than males. Unlike males, females apparently tend to spend most of their time on the host's web rather than travelling around (Chapter 1). Consequently, being able to feed with the host may be more important to females than males. Because it may be more important for females to exploit hosts effectively, females may be more predisposed to solve problems in this environment than males.

GENERAL DISCUSSION

In this study I provide evidence that *A. antipodiana* may be able to modify their foraging behaviour. In regards to araneophagy, males in particular were able to respond to the presence of spiderlings and become more efficient at capturing them. In regards to kleptoparasitism, females in particular improved their ability to solve problems associated with obtaining food captured by the host.

Thus *A. antipodiana* appear to be able to modify both routine (kleptoparasitic) and opportunistic (araneophagic) foraging methods. However, the amount of modification appeared to differ between the two feeding methods: changes to araneophagic behaviours enabled *A. antipodiana* to use another food source (spiderlings) whereas changes to kleptoparasitic behaviours only 'fine tuned' this foraging behaviour. Thus an opportunistic feeding method appeared to be subjected to a more drastic behavioural modification than a more common feeding method.

Such differences in an animal's ability to modify common and uncommon foraging techniques are not unprecedented. Sheehan and Shelton (1989) working with *Diaeretiella rapae* (a parasitoid that attacks aphids on 2 plant species) found that past experience affected plant examining behaviour only on the plant not commonly examined. This indicates that, in this species as in *A. antipodiana*, an uncommon feeding method appears to be more prone to behavioural modification.

The behavioural plasticity associated with the opportunistic feeding method (araneophagy) can result in an important change in the foraging behaviour of *A. antipodiana*. That is, it enables *A. antipodiana* to exploit effectively another food source (spiderlings) should they become plentiful. Consequently, it enables *A. antipodiana* to adjust to current environmental conditions.

However, the method by which this exploitation was achieved appears to be very simple. Basically, *A. antipodiana* appear to 'switch' from losing

the ability of catching spiderlings if they are not exposed to spiderlings during their critical period, to retaining their ability if there are spiderlings around. Thus in araneophagy, *A. antipodiana* seems to adhere to the 'use it or lose it' philosophy.

Nevertheless, it remains unclear why it would be advantageous for *A. antipodiana* ever to lose the ability to catch spiderlings. Perhaps retaining a foraging behaviour that may not be necessary may 'tie up' resources that could be put to better use elsewhere. However, more work is needed to clarify this problem.

The fact that *A. antipodiana* used such an apparently 'simple' method for such a major change is very revealing, and seems to indicate that learning in *A. antipodiana* is heavily constrained. That is, whenever possible, *A. antipodiana* may use the least amount of learning required in order to solve a problem.

Alternatively, the behavioural plasticity associated with the common feeding method (kleptoparasitism) resulted in only a minor behavioural adjustment, but involved a more refined method of behavioural modification. In the case of araneophagy, simple exposure to the foraging stimulus apparently triggered an all-or-nothing response. In kleptoparasitism, this was not the case. Instead, *A. antipodiana* had to associate a particular problem (not being able to reach the food) in a particular situation (on the 'wrong' side of the web) with the appropriate response (moving around to the 'correct' side of the web). Thus this form of behavioural modification appeared to be more complex than those associated with the 'improvement' of araneophagy.

The form of behavioural modification used in kleptoparasitism may enable *A. antipodiana* to 'fine tune' its behaviour to different host species. *A. antipodiana* is not only found in New Zealand, but also in Australia, where it kleptoparasitizes other hosts such as *Nephila maculata* (Mascord 1991), a particular large orb weaving spider. When feeding with a

large *Nephila maculata*, *A. antipodiana* does not need to go around the web to the opposite side to gain access to the foodbundle because the foodbundles of *N. maculata* are so large (pers. obs.). As a result, changing sides, which is useful on the webs of *E. pustulosa*, may be unnecessary when feeding with *N. maculata*. However, there are probably idiosyncrasies of *N. maculata* to which *A. antipodiana* may need to fine tune its behaviour. Consequently, some degree of plasticity may be important in order for *A. antipodiana* to overcome problems specific to its particular host. More work is needed to examine this possibility.

During its lifetime an animal faces many problems. It would seem practicable for an animal to evolve set responses for each of a series of predictable problems, the only limit being the number of 'solutions' an animal can store and sort. If, however, an animal frequently faces novel, unpredictable problems, then it may not be practicable to use 'pre-programmed' solutions. For an animal that faces unpredictable circumstances, an ability to learn would enable an animal to develop, during its lifetime, an appropriate response to each unpredictable problem. In the foraging behaviours of *A. antipodiana*, variations of both of these approaches appear to be used. That is, it appears that *A. antipodiana* may have a pre-programmed solution to the 'problem' of catching spiderlings, but perhaps not enough 'storage space' to retain such a program if it is not going to be useful. *A. antipodiana* also appears to use learning to derive an appropriate response to unpredictable problems associated with feeding with the host.

In this paper I have presented evidence of two means by which *A. antipodiana* may adjust behaviourally to its foraging environment. That is, *A. antipodiana* seems to have a 'critical period' which enables it to retain uncommon foraging behaviours, should they be useful, and *A. antipodiana* seems to have the ability to solve certain problems associated with obtaining food kleptoparasitically. Thus study adds to the

mounting evidence that invertebrates - even very small ones - are sometimes capable of performing learning feats similar to those more often associated with vertebrates.

SECTION IV

Discussion

CHAPTER 8

Theoretical aspects of learning and intelligence**ABSTRACT**

Intelligence and learning are terms that have often been difficult to define. In this chapter I first discuss some of the characteristics of intelligence, then I suggest my own definitions of learning and intelligence, and finally I compare my definitions with those provided by other workers. I define intelligence as the ability to 'link' together or associate ideas or behaviours in order to solve problems. I define learning as "any process in which the organization of an animal's behaviour is in part determined by some specific prior experience". I derive from these definitions that learning requires both memory and association. Consequently, I argue, all forms of learning must require some degree of intelligence.

I conclude that intelligence is probably best viewed as a qualifiable entity that varies among animals rather than an all-or-nothing characteristic which some animals express fully and others do not have at all.

INTRODUCTION

Although most lay-people will tell you that they 'know' what both intelligence and learning mean, the concepts to which these terms refer, especially 'intelligence', are actually very nebulous. In fact, when workers discuss intelligence, they do not usually offer a definition (e.g. Weiskrantz 1985) and it is assumed that the reader 'knows' what

intelligence is.

Additionally, discussions of learning or intelligence are usually focused on 'higher' vertebrates (e.g. Roper 1983, Jerison 1985, Johnston 1985, but see Griffin 1985, Hodos 1982). This occurs for a number of reasons. Workers tend to believe firstly that any evidence of learning in small invertebrates is so negligible that it can safely be ignored (e.g. Davey 1989) or, secondly, that the way in which invertebrates function is so foreign to the way that vertebrates function that it is pointless to compare the learning or the intelligence of the two groups (Hodos 1982).

The aim of this chapter is to first provide a thorough analysis of learning and intelligence in an effort to clarify these two terms. The second aim is to show that these terms are applicable to both vertebrates and invertebrates.

In order to realize these aims, I will first discuss some characteristics of the term 'intelligence', and shall define learning and intelligence. Next, I will compare my definition of 'intelligence' with definitions provided by other workers. Finally, I will discuss some constraints on both learning and intelligence.

DISCUSSION

1 Some characteristics of the term 'intelligence'.

The term 'intelligence' is nebulous and difficult to define. This is largely the result of two factors. Firstly, definitions of intelligence tend to be, perhaps out of necessity, broad; and secondly, the word 'intelligence' is used in two totally different ways.

The two different manners in which intelligence is used are: either as a quantifiable feature; or as a quality of the animal. That is, some animals or people are discussed as though they possess 'more' or 'less' intelligence than others; while concurrently, intelligence can be treated as an absolute (all-or-none) characteristic. For example, some workers

refer to particular animals or people as simply 'intelligent' or simply 'not intelligent'.

The second manner in which intelligence is used (that is, treating intelligence as an absolute) has perhaps developed out of the first. That is, once an animal is regarded as having a certain threshold 'amount' of intelligence, it is regarded as 'intelligent'. However, the 'amount' of intelligence required before an animal is regarded as being intelligent varies between different workers (e.g. Mackintosh et al 1985 in comparison to Macphail 1985). Consequently, this usage of the word appears to be highly subjective and, therefore, unhelpful for scientific purposes, and especially unhelpful for comparative studies of the intelligence of different animals.

The first alternative, which treats 'intelligence' as a thing that varies in degree between different animals is, perhaps, more representative of what is interesting about intelligence in the animal kingdom.

A broad definition of the word intelligence, and one that will be used here, is that intelligence is the ability to manipulate information, ideas or behaviours in order to solve problems. This definition is largely based on the school of thought that I have called the 'lateral thinking' view of intelligence (discussed in section 6.1). An example of this is the ability to associate quite distant concepts and so develop 'novel' solutions to novel problems.

2 A definition of learning

The ability to learn seems to be generally viewed as an important aspect of the concept of intelligence, but learning has also been difficult to define.

Papaj and Prokopy (1986) defined learning as a "reversible change in behaviour with experience." However, this definition is of limited use

because it is not clear that all non-reversible behaviours, such as those that are acquired with experience but not forgotten (e.g. learning to ride a bike or imprinting) should be excluded.

Johnston (1982) defined learning as "...any process in which, during species-typical ontogeny, the organization of an animal's behaviour is in part determined by some specific prior experience". This definition appears more useful, although restricting the definition of learning to 'species-typical ontogeny' does not appear justified. This definition excludes 'exceptional' learning, which is learning that, although unlikely to occur in the normal course of a species' development, can nevertheless occur under certain non-normal conditions (e.g. Pepperberg 1990). Exceptional learning, despite not being species-typical, may play an important role in the cultural development of a species (e.g. humans).

Perhaps a more useful definition of learning is to use Johnston's definition, but exclude the clause 'species typical ontogeny'. Doing this, learning is then defined as "any process in which the organization of an animal's behaviour is in part determined by some specific prior experience".

If learning is defined in this manner, then the definition of 'experience' becomes critical. 'Experience' may be defined as an event or incident in which an animal has participated. In the manner in which I am using it in the above statement, 'experience' also implies that the animal remembers the event, or some aspect of the event. Thus, inherent in this concept of experience, is the concept of memory.

However, the relationship of memory to 'experience' is not straight forward. In order for an animal to 'learn from its experiences', it does not need to remember the experience itself, but it does need to remember the effect of that experience. For example, some humans are capable of using experience to solve a puzzle, yet have no memory of acquiring the specific knowledge of how to solve the puzzle - as far as they are

concerned they just 'know' the solution to the puzzle (Weiskrantz 1985). Thus the person's behaviour has changed as a result of experience, but the actual steps involved in solving the problem have not been remembered.

By emphasising that memory is an inherent part of the concept 'experience', the definition of learning suggested above (i.e. "any process in which the organization of an animal's behaviour is in part determined by some specific prior experience") seems to correspond closely to most workers' basic, informal understanding of what is meant by the term 'learning'.

If we use this definition of learning, then learning appears to require memory and association, by definition. That is, an animal must remember, or retain an impression of, an experience in order for that experience to alter future behaviour. Also, an animal must be able to associate this memory with a current problem. If an animal, when faced with a novel problem, cannot associate a remembered solution with the problem, it cannot be said to have learnt the solution to the problem.

2.1 The association/application component of learning.

One problem encountered when examining learning and intelligence in animals is that we cannot directly measure most important things that we are discussing. To learn a solution to a problem an animal must associate the solution with the problem. Yet, it is not possible for us to see the animal make this association. All we can see is the application of the association. That is, a monkey may associate climbing on a chair with reaching a banana, but it does not need to actually perform this behaviour to make the association. However, we must first see this application of the solution to the problem before we can accept that the monkey is able to make the association between climbing on a chair and reaching a banana. The fact that association can be inferred only through the animal's application of the association is a major constraint in the study of

animal learning and intelligence (Herrnstein 1985).

3 Different types of learning

In order to understand learning, people have tried many ways of classifying manifestations of learning. Morgan (1894) proposed three methods by which the evolution of learning can be classified: the method of levels, the method of uniform reduction, and the method of variation. The method of levels assumes that learning behaviours can be arranged as a series of levels, extending from less intelligent to more intelligent, with only the more intelligent animals exhibiting the highest levels of learning. The method of uniform reduction suggests that animals differ only in the amount of learning they can achieve, whereas the method of variation suggests that an animal's learning ability is linked solely to its needs: animals are not better or worse at learning, only different. Thus the method of variation implies that the learning abilities of each species of animal have "developed" individually to suit that species' needs. As noted by Johnston 1985, all current views on learning can fall into one of these three categories.

Initially, psychologists who studied learning followed the traditional learning theory approach, which emphasized concepts such as the general process theory. This includes the principle of equipotentiality, an approach that appears to fit loosely into Morgan's category of uniform reduction. The idea behind the general process theory was that all instances of associative learning obeyed the same basic laws (Roper 1983). Equipotentiality, on the other hand, essentially implies that any animal can learn almost anything. Under equipotentiality, instances where learning fails to occur are interpreted as mainly resulting from the limitations of the species' sensory or motor capacities (Roper 1983).

Copious evidence of species specific constraints on learning has undermined these concepts (Manning 1979, Hodos 1982). The extent of this evidence has strengthened the ethological view that learning, in different animal species, is intrinsically different, and has adaptively evolved in response to conditions unique to each species. This view is akin to Morgan's method of variation. However, although learning in different animals does, obviously, meet the specific needs of that animal, this ethological viewpoint ignores similarities that can be seen between different types of learning.

Another way in which people attempt to understand learning is to assign examples of learning to different categories. This is akin to the 'method of levels' proposed by Morgan (1894). Thorpe (1951) proposed different categories of learning to give order to the great range of learning abilities shown by animals. He discussed seven categories: habituation, conditioning, trial and error learning, insight learning, imitation and imprinting. The last two categories, imitation and imprinting, were discussed as special cases of learning. The remainder progress from what are generally regarded as the most simple to the most advanced types of learning (Thorpe 1951, Manning 1979).

Habituation is regarded as the simplest form of learning. When habituating, animals simply become progressively less responsive to a recurring stimulus. For example, pigeons habituate to the sound of pistols firing, and after a period of exposure no longer respond to pistol shots (Thorpe 1951).

'Conditioning' is the classical conditional reflex made famous by Pavlov. To use Pavlov's example (1928), a dog learns to associate the ringing of a bell with the presentation of food. Initially the dog only salivated when meat powder was put in its mouth. If the meat powder was immediately preceded by a bell, then, after a number of trials, the bell on its own was sufficient to cause the dog to salivate.

The third category, trial and error learning, is also called instrumental conditioning or operant conditioning. Here, the animal learns to associate a particular response with a particular reward. For example, imagine an experiment designed to determine if rats can associate pushing a lever with obtaining food. A rat moving around a special cage, called a Skinner Box, may accidentally stand on a lever (i.e., perform an 'operation'). The apparatus is set up so that when the rat stands on the lever, food appears. After a number of trials the rat learns that if it presses the lever, food will appear.

The fourth category is insight learning. This is where an animal makes intuitive jumps from one set of problems to another. For example, an animal is given a problem which it solves after a number of trials. It is then given a new problem the solution to which is conceptually the same as the other problem but is different in its details. After a number of similar problems (called learning sets), the animal takes successively fewer trials to solve new problems. Both trial and error learning and insight learning can be further divided into sub-categories.

Habituation, classical conditioning, trial and error learning, and insight learning have been regarded as a procession of levels of learning, going from very simple (habituation) to very complex (insight learning) (Manning 1979). Thus these levels provide a scale against which animals might be compared, in that animals better at learning may use insight learning, while those not as good at learning may be limited to classical conditioning. However, actually trying to compare animals by using this scale is difficult. For example, some animals are capable of all the levels of learning, but only in very restricted areas of their lives, whereas others are capable of all the levels of learning, and they can apply these forms of learning to virtually all aspects of their lives. If only the levels of learning attained by these animals were compared, then large differences in the animals' learning abilities would be hidden.

4 The interrelationship between learning and intelligence

What are the differences between learning and intelligence? Perhaps the most important difference is related to the manner in which memory is involved. A behaviour must be 'remembered' to be learned. That is, an animal must be able to remember a behaviour in order to later repeat that behaviour. Here, intelligence is broadly defined as the ability of an animal to solve problems by manipulating information, ideas, or behaviours. Consequently, memory is not necessary for an animal to behave intelligently. For example, an animal could manipulate information in order to solve a problem, but later not remember the manner in which it manipulated the information. As the animal has not remembered the manipulation that succeeded in solving the problem, it has not 'learnt' the manipulation. Thus an animal could demonstrate intelligence without demonstrating learning.

For an animal to display intelligence, the origin of the manipulated pieces of information is irrelevant. That is, the information manipulated does not need to be initially learned; it could even be innately 'known'. How the animal acquired the information is irrelevant to the concept of intelligence. What is important from the point of view of intelligence is how the animal manipulates that information.

The definition of intelligence provided above seems very similar to the definition provided for insight learning. In fact, workers have often used insight learning experiments when trying to 'test' for intelligence (Mackintosh et al 1985). However, it can be argued (Adams 1931, cited in Thorpe 1951) that all forms of learning involve some degree of insight. That is, in order for an animal to learn, it must link a behavioural response to a stimulus. For example, with habituation, a repeated stimulus elicits the response 'ignore'. In order for an animal to form this link between stimulus and response, some form of insight appears to be necessary. Consequently, all forms of learning may require a certain

amount of information manipulation, implying that all forms of learning may require a certain level of intelligence.

This has important implications. If all learning requires at least a degree of intelligence, then all animals that learn must have some degree of intelligence. As all animals learn to some extent, then intelligence lies along a continuum within the animal kingdom. For any given animal species, asking whether or not it is intelligent is not very meaningful. Instead, we should ask where it lies along this continuum.

5 Measuring intelligence

I have argued above that all forms of learning require some degree of intelligence. Consequently, the different ways of measuring learning (as identified by Morgan 1894) may be useful in efforts to compare the relative intelligence of different species. I propose that a useful means of comparing the intelligence of different animals may be to combine two of the "methods of learning" described by Morgan. These are the "method of levels" and the "method of uniform reduction". I argue that an animal is more intelligent if it can (1) use higher levels of learning, and (2) can apply these forms of learning to a number of different tasks.

Thus, I suggest that intelligence might best be measured concurrently along two different learning scales: 1) the number of situations to which learning can be applied, and 2) the complexity of the learning which can be achieved. Consequently, an animal's intelligence could fall anywhere within a two dimensional area indicating that the intelligence of different animals might take very different forms. For example, one animal may attain very high levels of learning in one particular area, but be very poor when it tries to learn in other areas. Another animal may reach a lower level of learning, but be able to apply this learning ability to a wider range of problems. Both these animals are intelligent, but they are intelligent in different ways. Neither is as intelligent as an animal that

can both reach a high level of learning and apply learning to a wide range of tasks.

Obviously, it would be difficult to compare directly and quantitatively the intelligence of animals that vary within this 2-dimensional area. Nevertheless, this approach would reveal the form of the animals' intelligence, and give a crude indication of each animal's 'degree' of intelligence.

For example, bees can be said to show a high degree of intelligence. They can develop 'second-order conditioning' (Menzel 1989) and may even be able to form cognitive maps (Gould 1986, but see Menzel 1989), even though these abilities seem to be limited to feeding behaviour. Bees are more intelligent, in this respect, than other animals that cannot achieve this level of learning. However, bees have a type of intelligence that is different from that of an animal that can not attain such a high level of learning, but can apply learning more generally.

The type of intelligence an animal has may largely depend on its environment. An animal that is an opportunist, exploiting a range of foods or conditions, might be expected to have a more generalized form of intelligence. Contrasting this, an animals that is very specialized (perhaps with one particular means of foraging) may be able to demonstrate high levels of intelligence in that one specific area, but its expression of intelligence may be restricted primarily to that one area.

A problem with this approach to measuring intelligence is that it is very reductionistic. Although the 2 learning scales may give us a 'rule of thumb' by which to compare animals, they still miss the essence of what is intelligence. Basically intelligence, like sociality (Chapter 3) is more than the sum of its parts. Intelligence is more than what measurements along these 2 scales will indicate. Nevertheless, approaching intelligence from this viewpoint does enable us to avoid some of problems associated with other approaches to intelligence.

5.1 Preconceptions of an animal's intelligence.

One of the problems of studying intelligence in animals has been the lack of clarity about what the concept of 'intelligence' is and the absence of a means of comparing intelligence in different animals. As a result, workers often use an 'intuitive' feeling of which animals should be intelligent and use these animals as a standard against which to compare the different learning abilities of other animals. If a result from a learning experiment does not match this intuitive preconception of where the animals studied should fit within such a scheme, then the usefulness of the learning test is questioned by the researcher.

A classic example of this occurred when Manning (1979) discussed detour behaviour (a type of insight learning). He stated "It is perhaps unwise to read too much into ordinary detour experiments because some insects show extraordinary ability to handle this type of problem." Here he apparently inferred that, because insects are capable of performing detours, the ability to detour cannot be a good indicator of insight learning. Such biases only inhibit arrival at a deep understanding of what learning and intelligence are.

The means of comparing intelligence suggested in this chapter may help us avoid this pitfall in two ways. First, acknowledging that there are different forms of intelligence enables us to see animals as intelligent in different ways (for example in a general sense or in a specific, highly developed sense) which cannot necessarily be directly compared. Secondly, the approach I advocate here may enable us to be more precise by identifying characteristics which indicate interesting examples of intelligence in an animal. Clearly, identifying these characteristics may help reduce the effect of prejudices which are largely based on gut feeling. In the case presented by Manning (1979), wasps appear to be as good as dogs at detouring, suggesting that, in this case, the wasp is in fact just as intelligent as the dog in this respect. However, the dog may

illustrate intelligence more generally than the wasp: this may be the interesting difference between these two types of animals.

6 Comparison to other definitions on intelligence

6.1 The 'Lateral thinking' view of intelligence.

Intelligence is often defined as a form of lateral thinking, or ability to manipulate information. My definition appears to incorporate this view. However, advocates of the 'lateral thinking' view of intelligence may disagree with my definition on two accounts. Firstly, not all will accept that all learning involves some degree of intelligence. Secondly, some authors may differ in the manner in which they use the concept of 'intelligence'. That is, rather than seeing intelligence as something that varies between animals, they may see intelligence as an all-or-nothing characteristic which animals either possess, or do not possess (see section 1).

Although many researchers who stress lateral thinking do see intelligence as lying along continuums (e.g., Herrnstein 1985), which is the view I take in this Chapter, others do not. Workers who do not see it as a continuum argue that intelligence is a characteristic which animals either have or lack. They argue that only the animals that are capable of lateral thinking have intelligence. Thus only animals that have evolved this particular level of learning ability are considered to be intelligent. That is, authors who take this position would argue that not all forms of learning require intelligence. They would argue that animals that are not capable of lateral thinking are not intelligent.

The more extreme advocates of this view may even believe intelligence in humans is not on a continuum with that found in other animals and that intelligence in humans is intrinsically different from that in animals (Terrace 1985, Macphail 1985). Often there is a tendency for researchers who hold these views to use one or two key behaviours as indicators of

intelligence. This problem was highlighted by Mackintosh et al (1985) who pointed out that much work comparing intelligence between animals concentrated on a single experimental paradigm (such as learning sets). This restricted approach makes it difficult to ascertain differences between animal species in intelligence. Consequently, some skeptics such as Macphail (1985-although he looked at a number of characteristics) claiming that there was no difference in intelligence between animals, either quantitatively (e.g. learning levels) or qualitatively (e.g. amount of learning).

6.2 Adaptation: the ethological approach to intelligence.

Another way in which some authors define intelligence emphasizes adaptive advantages to the animal. Workers who advocate this view of intelligence emphasise the fact that the form which intelligence takes is often largely dictated by the demands put on the animal by its environment (e.g. Menzel and Juno 1985). Such a view of intelligence could be called an ethologist's view, and has made a valuable contribution to the understanding of intelligence because it highlights environmental constraints on intelligence. However, as Roper (1983) points out, ethologists are traditionally more interested in the functional relevance of learning rather than its underlying mechanism. This contrasts with the definition of intelligence proposed here which tries to address the underlying mechanisms.

The ethological view of intelligence as expressed by Hodos (1982) is largely based on the definitions provided by both Romanes and Tuddenham. Romanes (1883) defined intelligence as the "capacity to adjust behaviour in accordance with changing conditions". Tuddenham (1963) stated that "intelligence is not an entity, nor even a dimension in a person, but rather an evaluation of a behaviour sequence, from the point of view of its adaptive adequacy. What constitutes intelligence depends upon what the

situation demands". Each of these advocates of an adaptive definition of intelligence emphasises the relevance of the behaviours to environmental demands. Apparently, they would argue that the more immediately advantageous or adaptive the behaviour, the more intelligent the behaviour.

Another example of this was provided by Hodos (1982) who conceptualized intelligence as "a general adaptive behavioural response to the pressures of the environment rather than as specific intellectual faculties...". Again, what is regarded as indicating intelligence is neither the ability to manipulate information nor the ability to link unrelated ideas, but the degree to which the behaviour is adaptive.

Other workers agree, although they may not formally define intelligence. For example, Olton (1985) stated that "[spatial] memory helps animals behave adaptively (that is, intelligently) in many situations" [his parentheses]. Thus he also strongly links 'adaptive' with 'intelligent' and even states that to behave adaptively is to behave intelligently. Menzel and Juno (1985) commented that "Marmoset intelligence... is whatever marmosets do, especially if it gives them an advantage over their competitors". This statement shows, in an extreme manner, the way the meaning of the term 'intelligence' can be distorted when it is linked to 'adaptation' to such a degree that intelligence has no independent meaning at all.

6.2.1 Intelligence is not equivalent to adaptiveness.

I do not accept the premise that intelligence is simply equivalent to adaptation skills for a number of reasons.

Learning may not be adaptively advantageous. The first reason is that a more intelligent animal that relies heavily on learning may, in fact, not have an adaptive advantage over less intelligent animals. Johnston

(1982) reviewed the costs and benefits of learning and found that, in many ways (he highlighted eight), learning can be adaptively disadvantageous. Disadvantages may include: delayed reproduction prolonged periods of juvenile vulnerability, increased parental investment in each offspring and developmental fallibility. These disadvantages emphasise that it is often more adaptive to have innate, accurately pre-set responses to an environmental problem rather than incur the costs carried by having to learn appropriate responses. For example, an animal that responds correctly and immediately to a predator may be better adapted to its environment than an animal which must learn the correct response to that predator and subsequently run the risk of being killed before it has accurately learned the appropriate response.

An increase in intellectual demands may not reflect a similar increase in adaptiveness. Another reason why intelligence should not be defined in relation to adaptation is that, even if a particular behaviour indicates a high degree of intelligence, it may still not be adaptive. For example, an animal that uses insight learning may appear to be highly intelligent if it solves a difficult problem related to feeding, but if, by concentrating on this problem, it ignores other food that might be easier to obtain, then this behaviour might actually be maladaptive.

Intelligence is a certain class of abilities. Ascertaining the intellectual characteristics implied by a behaviour is quite separate from understanding the adaptive significance of the behaviour. It is not necessary to say that a behaviour has adaptive significance in order to conclude that it is an intelligent response.

A behaviour may imply intelligence and be adaptive for two different reasons. A third reason why intelligence should not be confused with adaptiveness involves looking closely at the characteristics of behaviours

that are regarded as both highly adaptive and intelligent. Often when people attribute both intelligence and adaptiveness to a behaviour, they think they are attributing intelligence and adaptiveness to the same thing when in fact they are attributing intelligence and adaptiveness to different aspects of that behaviour.

For example, acorn woodpeckers can store hundreds of acorns on the forest floor, and then, by memory, retrieve these acorns months later. This behavioural sequence is clearly adaptive, but whether it is an example of intelligence is a separate question. It is adaptive because it provides the animal with food during the winter months when food is scarce. It is also an example of intelligence because of the impressive memory abilities the bird required to relocate the seeds. Thus these different aspects of the same behavioural sequence enable us to conclude that this sequence illustrates both intelligence and adaptiveness. Thus adaptiveness is not equivalent to intelligence, even in this 'classic' example.

6.2.2 Invertebrate intelligence and exceptional learning.

Another reason why I disagree with the ethological view of intelligence is that it underrates the importance of exceptional learning, and tends to belittle invertebrate intelligence. This is well illustrated by the passage in Corning et al. (1976 cited in Hodos 1982) Corning et al were discussing an annelid which could learn associatively. They comment: "The imposition of vertebrate biases on invertebrates predisposes thinking that what is intelligent behaviour for the vertebrate must be a useful and desirable capacity in the invertebrate... For example, ...in annelids the existence of [associative learning] may prove to be of much more significance to the animal behaviourist than to the worm. While it may well be that worms can learn associatively, the demands of their normal environments seldom, if ever, actually require that they do so..."

Although Hodos (1982) applauded this comment, it illustrates two other unfortunate problems with the ethological approach. First, it down-plays the importance of exceptional learning in the worm, and secondly it implies that intelligence in invertebrates must be intrinsically different from that in vertebrates.

Exceptional learning is learning that is not required in the animal's natural environment, but which the animal, nevertheless, can still perform (Pepperberg 1990). Exceptional learning is common in rats, monkeys, pigeons and parrots and it has been one of the hallmarks of our own cultural evolution. Not only may the skills revealed in exceptional learning be of the utmost importance should conditions change, but it is intrinsically interesting that animals can perform these behaviours without giving the animal any selective advantage.

The second problem with the passage quoted from Corning et al (1976) is that it implies the view espoused by the ethological approach that invertebrate intelligence must be different from vertebrate intelligence. That is, it says that what is intelligence for vertebrates is unlikely to be useful and desirable for invertebrates. Because the ethological view ties intelligence to adaptation to the environment, and invertebrates tend to interact on a more 'simple' level than vertebrates, workers adopting the ethological view of learning tend to see intelligence in invertebrates as intrinsically different from that in vertebrates. This is not necessarily so, and will be argued against later in this Chapter.

6.2.3 The anthropocentric nature of intelligence.

One of the reasons why some authors support the ethological approach to intelligence is because they think that other views of intelligence are too anthropocentric (Menzel and Juno 1985) and based largely on behaviours highly valued by humans. These behaviours include: insight, reasoning, problem solving, concept formation, matching-to-sample, reversal learning,

learning set, and tool use (Hodos 1982). However, these behaviours (except, perhaps, tool use) do seem to illustrate highly developed intelligence.

Maybe our ideas about intelligence are, indeed, anthropocentric. Humans do rely heavily on high-level learning and this has undoubtedly contributed to humans being evolutionarily successful. It is likely that through the course of our evolution we have come to rely heavily on intelligence to survive. Consequently, the behaviours we exhibit may be those at the current pinnacle of intelligence. If this is so, then is there anything wrong with the basic concepts about intelligence being anthropocentric?

Anthropocentrism is a problem. Intelligence is highly valued in our society, and naturally, we want to bestow this high value upon ourselves by classifying humans as highly intelligent. Consequently, we may try to classify all of our attributes as examples of intelligence whether they really are examples of intelligence or not. Consequently, some behaviours have been used as evidence of intelligence simply because they are commonly used by humans (Menzel and Juno 1985, Hodos 1982) rather than for any other reason. Hence it is important that caution is exercised, as very human-typical behaviours may be described as 'intelligent' simply because they are typical of humans.

7 Intelligence incentives: the effect of intrinsic and extrinsic rewards on learning

Motivation plays an important role in learning. Basically, if an animal is not 'motivated' to perform a behaviour, it is not going to associate other behaviours with that behaviour. For example if a rat is not inclined to push levers, it is not going to learn to associate lever pushing with food. However, the form that motivation can take varies. For example, an animal may be motivated to perform a behaviour in order to

receive extrinsic rewards. Alternatively, an animal may perform a behaviour because it gets a reward from (or 'enjoys') simply performing the behaviour (an intrinsic reward).

Recent work has shown that these two different forms of motivation have different influences on the learning behaviour of animals. This is well illustrated in work on teaching chimpanzees 'English' (Gardner and Gardner 1985). In this area of research it has been difficult "to distinguish between a lack of ability and a lack of incentive to perform the task at hand" (Cheney and Seyfarth 1985). To encourage the chimpanzees to learn English, two different protocols have been used. One protocol is to use extrinsic factors to encourage communication, such as food, or gaining access to an object. The work of Terrace and also Premack has been largely devoted to this approach (see Lieberman 1984 and Bickerton 1990 for reviews of ape language studies). The other protocol is to use intrinsic factors as the reward. Intrinsic factors are where the behaviour itself is rewarding. The approach of the Gardners has always been via this method; and more recently Savage-Rumbaugh and others have adopted this approach (Savage-Rumbaugh et al 1985).

What has become apparent is that the animals which are motivated by intrinsic factors do considerably better than those motivated by extrinsic factors (Gardner and Gardner 1985, Savage-Rumbaugh et al 1985). So the factors used to encourage the animals to learn has a profound effect on the animal's ability to learn.

8 Constraints on intelligence

Constraints are factors that limit an animal's ability to learn. As such, they are vital to the well-being of the animal. An animal whose learning is not constrained in any way might associate two unrelated events (e.g., birds flying overhead with impending rain) which can be to its detriment rather than to its advantage. Constraints are the means by

which an animal directs learning to where it is necessary and useful.

Constraints range from adaptive responses to developmental or structural limitations of the animal's brain .

8.1 Environmental constraints.

Constraints which have attracted attention in recent years are those that appear to be adaptive responses to the environment. Here, the type of intelligence that an animal develops appears to be largely influenced by the environmental conditions that the animal faces. The importance of these environmental constraints on learning has been highlighted by the ethological view of intelligence which has provided us with the most comprehensive survey of these constraints. A clear example of an environmental constraint is an animal that relies heavily on sound, and is unable to associate two shapes because of a limitation in its visual perception.

Another way in which adaptation to the environment constrains an animal's ability to learn is that it can influence what an animal will or will not associate. For example, a hummingbird will readily learn to move from the rewarded target to a new target (shift learning), but has difficulty learning to stay at a rewarded target (stay learning) (Beecher 1988). This reflects environmental demands on a hummingbird to move from one flower to another. Other forms of environmental constraints of this kind include taste aversion learning (a taste can be associated with being sick whereas a light flashing cannot; Johnston 1985) and other instances where animals are more inclined to learn associations to events that make ecological sense for their particular environment.

8.2 Structural constraints.

Structural constraints are where the characteristics of the brain limit what the animal is capable of learning. An important example of

this, which will be discussed in some detail, is brain size.

8.1.1 A special case of a developmental constraint: brain size.

Jerison (1973) had an interesting view of intelligence which he has reiterated since (Jerison 1985): "I propose that encephalization is, in fact, the fundamental trait and that it may be fruitless to seek finer correlates of intelligence". So in short, Jerison concludes that brain size is the key to understanding intelligence- the larger your brain, the more intelligent you are. He even argues that no other measurement of intelligence is needed.

But, let us consider the relationship between brain size and intelligence. If brain size is as important to intelligence as Jerison states, then the size of an animal's brain is a serious developmental constraint on the intelligence of an animal. Is this claim justified? Also, are there major structural differences between invertebrate and vertebrate brains, irrespective of size differences?

Although Jerison's view that brain size alone determines intelligence is extreme, the notion that brain size increases with intelligence was as popular in the past (Snell 1891, cited in Jerison 1973) as it is today (Falk 1990, Krantz 1990). Nevertheless, there has still been strong opposition to this view (e.g. Hodos 1982) with a large body of evidence against this hypothesis coming from studies of humans (Tobias 1971, cited in Falk 1990).

To try to ascertain the relationship between brain size and intelligence, Russell (1979) compared different techniques of measuring brain size against intelligence within the vertebrates. These techniques included those which took into consideration the importance of different parts of the brain and differences in body size. That is, this technique expressed brain size in relation to body size, the simplest relationship being a direct ratio of brain weight to body weight. Intelligence was

formally defined as "increasing complexity and adaptiveness of behaviour". No quantitative estimates of intelligence were provided, although different measurements of intelligence were discussed at the end of the paper. Animals were ranked in accordance with the particular technique of measuring brain size that was under scrutiny, and this ranking was compared with an intuitive ranking of species by intelligence. Russell concluded that changes in brain size were only meaningful within each particular vertebrate taxa. He did not examine non-vertebrae taxa.

I know of no comprehensive study of invertebrates in which a relationship between brain size and intelligence has been investigated. However, there have been studies on the relationship between brain size and intelligence within smaller invertebrate taxa. For example, Cole (1985) looked at the display repertoire of different species of ants, and related display repertoire to head size. He found that larger ants also had large display repertoires.

These results suggest that brain size has an effect on intelligence, at least in a broad sense, between species. If this is so, then, in terms of intelligence, invertebrates are greatly disadvantaged when compared with vertebrates. For example, the brain of a female orb web spider has only 30,000 neurons (Foelix 1982), whereas that of a human has 100,000,000,000 (Aleksander and Morton 1990). But is brain size the only factor that differentiates invertebrates from vertebrates, or are the structures of their brains inherently different?

Traditionally, the brains of invertebrates and vertebrates have been viewed as inherently different. In fact, the neural networks in invertebrates are often not even deemed worthy of the term "brain". This form of 'apartheid' is understandable given the gross structural differences between the brains of invertebrates and vertebrates. Firstly, the neurons of vertebrates are more centralized than those of invertebrates. In invertebrates, ganglia along the length of the body play

a major role in controlling the body parts with which they are associated. These ganglia are also capable of learning. Additionally, the brains of vertebrates are arranged differently from those of invertebrates.

So the brains of invertebrates and vertebrates differ in general structural detail. Do they also differ at the neuronal level? Are the neurons of invertebrates and vertebrates intrinsically different? Basically, the neurons are the same, except that at least in the case of the small invertebrates, brain characteristics have evolved apparently to compensate for the severe limit on space (Wilson 1971). For example, invertebrate neurons have smaller cell bodies, shorter axons, reduced myelin sheathes, and shorter dendritic arborizations. These features increase the compactness of the intermingled dendritic arborizations, and increase the total number of neuronal connections possible (Wilson 1971). Consequently, they appear to be designed to compensate for the limited amount of space in the bodies of most of these small animals and for the small number of neurons present in many invertebrate brains.

9 The relationship between intelligence and brain function

Throughout the history of brain research there have been two classes of theory: localization theories (where distinct parts of the brain have been envisaged as having distinct functions) and diffusion theories (where most of the brain is envisaged as being important in the majority of functions). These theories have been the focus of intense debate and each has had its turn at being 'in vogue' (For a recent, thorough review see Star 1989).

During the 1860s, localization theories took hold, due to the work of Broca, Jackson, Ferrier and others, and they have more or less continued until the present day despite large discrepancies between predictions and actual findings which occurred as early as the 1860s. The localization legacy can be seen today when we talk about 'the speech area' and use

other such popular terms (Star 1989).

It is interesting that the metaphor of brain function, the serial computer, ties in well with the localization theories. This view holds that memories can be identified as distinct blocks of the brain, analogous to distinct areas on a silicon chip - if you remove the chip you remove that memory. Early researchers on artificial intelligence thought that human brains operated in a similar way to serial computers and that it was only a matter of time before we could build computers that could think like us (Penrose 1989). However, work has shown that in order for computers to do some of the simplest tasks that humans take for granted, such as understanding speech and driving a car, they require inordinate amounts of computer 'brain' space. This is because, whereas a serial computer has to be programmed for all the possible problems or outcomes that may occur, humans and other animals can function well on incomplete information (Skarda and Freeman 1987).

Since the 1980s there has been a strong revival in another type of neural modeling called connectionism or parallel distributed processing models. These fit in well with the old diffusion models, and appear to be heralding a return to a more holistic approach to understanding the brain.

The idea behind neural networks is that neurons are all interconnected. Learning occurs when connections between neurons are strengthened (Aleksander and Morton 1990) and a memory is represented by a space-time pattern of neural activity within the net. Skarda and Freeman (1987) working with olfaction in rabbits, illustrated this by showing that every neuron in the olfactory bulb of the rabbit is used when the rabbit discriminates between different smells. They showed that neural activity is always going on in the brain, and suggest that this activity will never fall into a set pattern and so allows the rabbit rapid and unbiased access to every identified smell on each inhalation. A learnt smell is represented in neural activity by a limit cycle attractor which acts like

a sink-hole, attracting neural activity. New limit cycle attractors are formed as new smells are learnt. Smells not recognized 'fall' into a 'chaotic well' (Skarda and Freeman 1987).

This view on how the brain functions has major implications, as it shows how all learnt categories may be immediately available to the animal; it shows a method by which memories can be created; it shows how the concept "don't know" can be represented in the brain; and it shows "there is no search through a memory store" (Skarda and Freeman 1987). But more importantly, this model indicates that not all of the neurons need to be triggered for a correct response to be given (the system can operate on partial information) but that the complete network of neurons are important for each memory.

This model emphasises the importance of the whole brain for each learning activity. This is important for two reasons.

First, it suggests that the gross organizational differences between invertebrates and vertebrates may not have much bearing on differences between the two groups in intelligence. This is because brain structure is not so important. If information processing requires the complete network of neurons, then there is no particular part of the brain where memories are stored, or where associative learning occurs.

However, the fact that invertebrate brains tend to be less centralized may be detrimental to their information processing. Distributing neurons throughout the body makes it more difficult for each neuron to connect with each other neuron. Consequently, the number of interconnections between neurons in invertebrates may be fewer relative to vertebrate neurons.

Secondly, this model illustrates how brain size may affect intelligence: the larger the brain, the more possible interconnections possible, the greater the ability to remember things, and the greater the chance of associating different things. Because possible connections

between cells increase exponentially as the number of cells increases, the limiting effects of brain size may be felt more acutely at the smaller end of the scale than the larger end. For example, the central nervous system of a female orb web spider contains 30,000 neurons (Foelix 1982) whereas the human brain contains 100,000,000,000 neurons (Aleksander and Morton 1990). Thus the number of possible connections the spider CNS is 4,500,015,000 whereas in the human it is 5,000,000,000,050,000,000,000!

9.1 Exceptional learning.

Current work (e.g. Skarda and Freeman 1987, Freeman and Skarda 1990) suggests that brains do not allocate separate areas for different learning functions. The more holistic view of the brain implicit in this current work has ramifications for our understanding of the development of exceptional learning. This is because the holistic approach indicates that brains do not have to develop more 'advanced' parts in order for the individual to become more intelligent; they just need to get bigger. Thus a brain may get larger for some reason unrelated to learning, and as a result of increasing in size, the animal could become more intelligent.

For example, Fialkowski (1990) has proposed a theory on human intelligence which is strengthened by the current holistic, connectionist view of how brains function. He argues that human brains increased in size to compensate for the malfunctioning of parts of the brain due to heat stress. Thus he argues that the increase in our brain's size did not come about as a result of selection pressures specifically for intelligence; instead, by acquiring a larger brain, we became more intelligent. If this argument is correct, then a substantial part of what we regard as human intelligence may have actually originated as exceptional learning instead of adaptive learning.

CONCLUSION

Intelligence and learning are terms that have often been difficult to define. In this chapter I have argued that intelligence is the ability to 'link' together or associate ideas or behaviours in order to solve problems. As learning has both a memory component and an association component, then all forms of learning require some degree of intelligence. Thus intelligence is probably best viewed as a quantifiable entity that varies among animals rather than an all-or-nothing characteristic which some animals express fully and others do not have at all.

This view of intelligence has many ramifications. Firstly, it varies from the 'ethologist' view of intelligence which emphasises the adaptive nature of many expressions of intelligence. I argue that the adaptiveness of a behaviour is quite a separate issue from whether that behaviour is an example of intelligence. An example of intelligence does not need to be adaptive and could even be maladaptive.

Nevertheless, the ethological approach to intelligence has been important because it has emphasised the environmental constraints on learning and intelligence. Constraints play a major part in the expression of intelligence and learning in animals. One of the more interesting constraints is brain size, which is a structural constraint. Ideas which link brain size to the ability to express intelligence fit in well with ideas presented here, as do current holistic approaches to the manner in which the brain functions. The expression of learning and intelligence varies greatly between different animals, but perhaps they are all manifestations of the same basic process.

CHAPTER 9

Spider intelligence: learning and problem solving in
Argyrodes antipodiana

ABSTRACT

The role of learning and intelligence in the social behaviour, foraging behaviour and during male-male competition in *A.antipodiana* is analysed using the definitions developed in Chapter 8. I conclude that *A.antipodiana* is limited in intelligence. Nevertheless *A.antipodiana* deals most effectively with the problems of environmental variability by ignoring as much of this variability as possible. By 'ignoring' the variability, *A.antipodiana* reduces the amount of behavioural plasticity it needs in order to cope with its environment. However, in some cases it appears that *A.antipodiana* cannot ignore the variability. In these cases, *A.antipodiana* is capable of quite advanced forms of cognition, but these instances are narrowly channeled to specific situations. Consequently, although *A.antipodiana* has limited intelligence, it is still able to respond very effectively to the variable conditions it encounters. In addition, the ideas about intelligence and learning developed in Chapter 8 prove to be useful in the analysis of the behaviours of *A.antipodiana*.

INTRODUCTION

Discussions of intelligence and learning are usually limited to higher vertebrates, (e.g. Roper 1983, Jerison 1985, Johnston 1985, but see Griffin 1985, Hodos 1982). This occurs for a number of reasons. It is commonly believed, firstly, that any evidence of learning in small

invertebrates is negligible and can safely be ignored (Davey 1989) and, secondly, that the way in which invertebrates function is so foreign to the way that vertebrates function that it is pointless to compare the two anyway (Hodos 1982). In this Chapter, I go against this train of thought and analyse learning and intelligence in the small invertebrate, *A. antipodiana*.

The work presented in this thesis focuses on establishing what forms of behavioural plasticity and learning occur in *Argyrodes antipodiana*. In this chapter, I examine the behavioural plasticity exhibited by *A. antipodiana* by using the ideas on intelligence developed in Chapter 8. I discuss: (1) The interrelationship between behavioural plasticity and sociality; (2) Behavioural plasticity associated with competition; and (3) behavioural plasticity associated with feeding. The goal of this analysis is to examine the extent to which theory related to intelligence and learning account for these three aspects of the behaviour of *A. antipodiana*

DISCUSSION

1 The Interrelationship Between Behavioural Plasticity and Sociality

A prevalent theory in the study of vertebrate intelligence (especially in reference to human evolution) is that living in social groups increases intelligence. For example, Jolly (1966) suggested that human intelligence arose from the need to prosper in a complex social environment. This view is popular and has been supported by many people (e.g. Cheney and Seyfarth 1985, Harcourt and Stewart 1987). The key to the argument is that the development of sociality within an animal group greatly complicates an animal's environment so that it needs to increase its intelligence in order to cope with this increase in complexity.

Apart from the noteworthy discussion of this idea in relation to Hymenoptera (Wilson 1971), the hypothesis of sociality affecting intelligence has rarely been applied to invertebrates. Here, I examine

this hypothesis in relation to *A.antipodiana*. *A.antipodiana* naturally occur in small groups, the members of which regularly interact with each other. Has living in social groups been a factor in the evolution of intelligence in *A.antipodiana*?

When looking for evidence of a link between 'sociality' and 'intelligence', the first step is to define these two terms. A definition of 'intelligence' was proposed in Chapter 8: intelligence is the ability to solve problems by manipulating information, ideas or behaviours. Sociality was discussed at length in Chapter 3. Therefore, I will only briefly discuss sociality and its relationship to *A.antipodiana* before discussing sociality and intelligence in relation to *A.antipodiana*.

1.1 Sociality and *A.antipodiana*.

Sociality is a notoriously difficult term to define (Chapter 3). Most of this difficulty arises because sociality can only be defined in behavioural terms even though it itself is not a behaviour (Baylis and Halpin 1982). In fact, a social group, unlike other groups, appears to be a group with its own 'identity' (Chapter 3). That is, the behavioural characteristics of the group is greater than the sum of the behavioural characteristics of the individuals which make up the group. However, a group having its own 'identity' is an imprecise concept. Consequently, workers often resort to analysing the behavioural characteristics that are often associated with social groups. Four frequently discussed behavioural characteristics are interattraction, tolerance, cooperation, and recognition. In Chapter 3, I argued that, of these four, tolerance seems to be key in understanding spider sociality. I argued that, although spiders demonstrated interattraction, there is little evidence that they are capable of individual or group recognition, or even cooperation. However, all forms of spider sociality may be effectively compared by analysing the degree to which spiders can tolerate each other.

Nevertheless, the degree to which spiders vary in level of tolerance is not a linear relationship because tolerance can vary in at least three different ways. For example, spiders may vary in the actual distance between conspecifics that they will tolerate; their tolerance towards conspecifics may vary with reference to stages in their lifecycle, and their tolerance may vary with reference to their behavioural activity.

In New Zealand, *A.antipodiana* form small mixed groups around the webs of their larger host, *Eriophora pustulosa*. Individual *A.antipodiana* from these webs regularly re-interact with the same individuals within a 4 m area and these groups seem to persist for a reasonable period of time.

As in other spiders, sociality in *A.antipodiana* is largely based on interattraction and tolerance, there being no evidence of recognition or cooperation. *A.antipodiana* are tolerant of each other when resting, but largely intolerant when feeding. Thus, the tolerance *A.antipodiana* varies in relation to behavioural activity.

1.2 Sociality of *A.antipodiana* and use of intelligence.

As the sociality of *A.antipodiana* seems to be largely based on tolerance, *A.antipodiana* probably avoids many of the 'intellectual demands' placed on some other animals in social groups. For example, unlike other animals, *A.antipodiana* do not appear to learn to recognize each other. Individual recognition is very advantageous in some social groups, as it enables an animal to respond appropriately to a particular individual, rather than treat all individuals as the same. *A.antipodiana*, however, do not respond to conspecifics as individuals. Instead, the manner in which they interact with other individuals seems largely determined by their own current state (e.g. whether they are foraging, or whether they are on the hub or not; see Chapter 2).

Additionally, there is no evidence of cooperation.

Even the manner by which *A.antipodiana* modify their level of tolerance of conspecifics when they are on the hub and away from the hub does not appear to be the result of learning. In fact, work in Chapter 2 indicates that this conditional strategy is probably innate rather than learned.

Consequently, there is no evidence of *A.antipodiana* learning in a social context. If we define 'intelligence' as the ability to manipulate information, ideas or behaviours in order to solve problems (Chapter 8), then it appears that there is little evidence of intelligence in the social behaviour of *A.antipodiana*.

1.3 Sociality, intelligence and insects.

At the beginning of this section, I mentioned that a prevalent argument in the evolution of human intelligence is that strong selection pressures for intelligence came from the complex social environment in which pre-historic humans lived. This is an interesting hypothesis and it may be useful to see if there is any evidence to support it in other species.

Some of the most complex societies that exist today are those of insects. These societies can contain many thousands of individuals, are very highly structured, and have well developed communication systems. However, from studies of Hymenoptera, we know that solitary species have mental capacities that appear to be at least equal to those of the eusocial species. For example, the solitary wasp *Ammophila* appears to be as good as dogs at solving detouring problems (Manning 1979). In addition, some species of solitary Hymenoptera have even developed individual recognition (e.g., sweat bees; Wcislo 1987), whereas eusocial species can only recognize castes. Thus, in the Hymenoptera, there is no evidence suggesting that sociality leads to increased intelligence (Wilson 1971).

This finding goes against the prediction that sociality would lead to an increase in intelligence in eusocial Hymenoptera. Consequently, it may be prudent to try to understand how intelligence does interrelate with sociality.

1.3.1 Sociality and intelligence.

Rather than seeing intelligence as the product of a complex social system, it may be more useful to see it as a constraint on the development of sociality at the level of the individual animal. That is, if the animal is intelligent, then the type of sociality that develops will involve a strong reliance on learning, whereas if the animal is not intelligent, then it will solve problems of sociality by means that do not involve learning. This argument may account for the type of sociality that has developed in social spiders. An important part of sociality is group cohesion; the means by which most animals enhance cohesion through recognition (Halpin 1980). Animals within a group recognize other group members and preferentially associate with these animals, while at the same time they recognize outsiders which they exclude from their group. Any form of recognition, however, requires some form of learning. Animals must learn the characteristics of their group that distinguish it from other groups. Social spiders have apparently evolved in a different way. They form very tolerant societies in which all conspecifics are accepted as group members. Spiders, therefore, appear to live in groups where the need to learn to recognize each other in order to maintain group cohesion is not necessary.

1.3.2 The interaction between sociality and intelligence.

The relationship between sociality and intelligence is not, however, a one-way street. Intelligence may influence the development of sociality, but sociality may also influence the development of intelligence. For

example, an intelligent species may evolve a society in which distinct culture is important. By developing a particular form of culture, an animal may have a society in which intelligent individuals benefit, and so in this context sociality may encourage evolution of still greater intelligence. Nevertheless, the species in which sociality originally developed would probably need a certain level of intelligence in order for a complex culture to develop in the first place.

A. antipodiana show little evidence of learning in the social context. This is interesting from two perspectives. First, *A. antipodiana* are able to learn in other areas of their biology (see Chapters 6,7). If sociality strongly encourages learning, then one may expect it to be at least as well developed in the social context as it is elsewhere in this animal's life. The second reason is that the ability to learn would appear to be advantageous to *A. antipodiana* in the social context. For example, individual recognition would probably be advantageous to an *A. antipodiana* competing for food because it would enable an *A. antipodiana* to respond more accurately to its competitor. That is, if it knew its competitor was aggressive, it could quickly back down (and not waste time competing) or, if it knew its competitor was timid, it would know to largely ignore it (and not waste time challenging it). Individual recognition would, in turn, enhance the development of sociality itself in this species.

Thus, it appears that in *A. antipodiana*, sociality has not enhanced intelligence. In fact it seems that the apparently limited intelligence of *A. antipodiana* may have even contributed to the restricted development of sociality in this species.

2 Behavioural Plasticity Associated with Competition

When male *A. antipodiana* compete for access to females, they are faced with an unpredictable situation in which they must make decisions. It is often argued that such situations are best dealt with by the animal using

learning and cognition skills. *A. antipodiana*, however, appears to keep the use of these skills to a minimum. *A. antipodiana* is able to reduce the use of cognitive skills, apparently because it simplifies the situation so that advanced forms of cognition are not necessary. One means by which *A. antipodiana* achieves this is by largely ignoring the current contest situation and basing its response to its adversary on its own motivation to compete. *A. antipodiana*'s motivation to compete may be affected by many unrelated factors such as its size, its degree of hunger, the number of previous contests in which it has been involved and its own past experience in contests.

2.1 Means of simplifying the contest.

2.1.1 The effect of size on contests.

It was found that the actual size of the two opponents influenced the degree to which contests escalated. That is, pairs of larger spiders were more likely to escalate their contests than pairs of smaller spiders (Chapter 5). This discrepancy was even apparent in naive spiders. Thus, this difference was not related to any characteristic of the current contest (such as the value of the resource, or a difference in the RHP: Resource Holding Power; sensu: Parker 1974) of the opponents, but to the internal characteristics of the animals themselves.

By basing its degree of escalation on its own size, *A. antipodiana* effectively reduces its need to assess the current contest. That is, if *A. antipodiana* is 'preprogramed' to escalate to a certain degree, it does not need to assess, from the current contest conditions, the degree to which it should escalate.

Large discrepancies in size between opponents also influenced the outcome of contests. That is, males that were more than 22% larger than their opponents were more likely to win contests. This result does, however, indicate some degree of assessment of the current contest and

will be discussed in more detail later.

2.1.2 The effect of hunger on contests.

In tests where hunger levels were uneven, smaller, unfed spiders had a better chance of winning contests against larger, fed spiders, than against larger, unfed spiders. That is, a difference in the hunger level of the two opponents appeared to delay the effect of weight discrepancy on the outcome of contests. For example, when both spiders were unfed, the larger spider tended to win when the weight difference was greater than 22%, but when the larger spider was fed, the larger tended to win contests only once the weight difference was greater than 30%.

Hunger level is known to affect the tendency of animals to compete for food (Barnard and Brown 1983, Hazlett et al 1975), as hungry animals in these competitions are more motivated to compete for food. However, it is surprising that hunger should affect tendencies to compete for females, as this makes little functional sense. The observed increase in competitiveness apparently occurs in response to the internal state of the animal which appears to be unrelated to the current contest conditions.

Thus it appears that the motivational condition, 'hunger,' actually increases the overall aggressiveness of *A.antipodiana*; and, by doing so, it appears to exert a major influence on the outcome of a contest to which it appears to be functionally unrelated.

The observation that hunger may affect aggressiveness in general in *A.antipodiana* has major implications. When workers observe contests, they usually relate the behaviour of the animals to the conditions of the contest. But if unrelated, internal factors like hunger are strong, then the behaviours observed in the contest may actually have little to do with either what the animals are competing for or the characteristics of their opponents.

2.1.3 Number of previous contests.

The contests of naive *A.antipodiana* generally escalated higher than the contests of *A.antipodiana* which had often competed for females (Chapter 5). Thus, it seems that *A.antipodiana* may habituate to partaking in contests for females. Consequently, the number of contests in which an *A.antipodiana* has been involved appears to influence its readiness to escalate. Thus, this form of habituation appears to be another means by which the characteristics of a spider can influence its behaviour in a contest, irrespective of the characteristics of the contest.

2.1.4 Winning and losing past contests.

Past experience at either winning or losing contests also influenced the behaviour of *A.antipodiana* in the current contest. Spiders whose previous experience was to lose contests lost interactions with similarly sized spiders whose previous experience was to win contests. Thus, these spiders were basing their response to the current contest on their experiences in previous contests. Responding in this way to past experience is a form of operant conditioning because *A.antipodiana* is associating a behavioural response to a situation. Using this type of learning in a current contest is advantageous because it mimics the effect of assessment (Chapter 6) even though it seems to require less reliance on cognitive abilities (see below).

Therefore, again it appears that the characteristics of the current contest (that is the size of the opponent or the quality of the contested resource) had little bearing on how the contestants interacted. *A.antipodiana* appeared to be relying mostly on internal influences to dictate their behaviour in the current contest, rather than in assessing the current situation.

2.2 Assessment.

All of the above influences on the contests of *A.antipodiana* serve to reduce the degree to which *A.antipodiana* needs to assess the current contest directly. Why does *A.antipodiana* appear to 'want' to reduce its reliance on assessment? I will argue that assessment is actually an advanced form of learning, and that by reducing the amount of assessment that it needs to make, *A.antipodiana* simplifies its contests and reduces its need to use higher cognitive processes. Thus, the factors that reduce the need for *A.antipodiana* to respond directly to the current contest conditions enable *A.antipodiana* to solve problems associated with contests (such as who will win the contest) by using only limited intelligence.

2.2.1 The cognitive aspects of assessment.

The ability to assess the RHP of an opponent seems to indicate an understanding of the concept 'more' and 'less'. Differentiating between 'more' and 'less' is likely to be a pre-numerical ability, and has been found in vertebrates, at least in chimpanzees, squirrel monkeys and rats (Pepperberg 1987). Bees have also been shown to differentiate between 'more' and 'less' (Gould and Gould 1982).

In male-male contests for access to females, it is usually assumed that males assess both the 'quality' and size of their opponents (e.g., Clutton-Brock and Albon 1979). In order to do this, a male would presumably need some understanding of its own size, and it would need to be able to assess whether the RHP of the opponent is smaller or greater than that of itself. Thus, the animal would need some understanding of quantity. Subsequently, the more similar the RHP of two contestants, the harder it would be to discriminate between them and the greater the demand on the animal's intelligence when attempting to tell them apart. This mental agility may be too 'costly' for an animal, or the animal may simply not have the mental attributes with which to do such comparisons.

The cost mentioned above can refer to the cost to the animal of using its brain. The brain is a very expensive organ to run as it uses a lot of energy (Johnston 1982). Related to avoiding this and other costs of using their brains, natural selection appears often to have favoured animals that avoid using advanced forms of cognition whenever possible.

For example, Dickinson (1985) reports that rats can exhibit purposeful and goal-directed behaviour (which are characteristics of insight learning). However, if a rat becomes 'overtrained', it still completes the task, but instead of solving the problem with insight learning, it simply responds reflexively to a stimulus to solve the problem. Thus, the animal appears to use a lower level of learning (associating a stimulus with a response) in preference to a higher level of learning (insight learning; Chapter 9).

Similarly, in humans, a common example of an attempt to avoid higher forms of cognition is illustrated when 'it goes wrong', such as when people who go to take off their shoes, find themselves in their pyjamas!

2.2.2 Assessment in *A.antipodiana*.

In the contests between *A.antipodiana* males, larger spiders were more likely to win contests when they were more than 22% larger than their rivals. Thus, it appears that *A.antipodiana* were able to assess, to some extent, the size of their opponents, indicating that they were capable of assessment.

However, *A.antipodiana*'s assessment ability appears to be limited in that they were capable of assessment only after the difference between the opponents became large (that is, greater than 22%). Presumably it is more taxing to assess differences between similarly sized opponents than between opponents that differ greatly in size.

2.3 Sneaky copulations and intelligence.

Another factor that may influence the response of *A. antipodiana* to the current contest is its ability to sneak copulations later, even if it loses the current contest (Chapter 4). This may reduce the advantage of winning the contest. However, interactions between the male who won the contest (the first male) and the male who lost but still tried to get copulations (the second male) appeared very complex and these interactions may actually require a certain degree of intelligence.

The first situation that may require intelligence is that faced by the first male when he must choose whether to mate with the female or chase the second male away. To understand this problem, let us consider the options available to a male when another male is courting the same female. A male in this situation may avoid or ignore his opponent and just try to mate with the female, or he may chase his opponent or disrupt his opponent's copulation attempts.

First males commonly chased second males away from the female. This approach, however, was disadvantageous for the first male because, in order to chase the second male, he had to terminate his own copulation attempts; and additionally, the second male always seemed to return after being chased. As an alternative, the first male occasionally ignored the second male and continued to court and copulate with the female.

Thus the first male appeared to be faced with a dilemma of whether to mate or chase. Attaining a solution to this problem may have required a certain degree of mental flexibility in that the first male may need to assess the situation and decide on which response is more appropriate.

The second situation that may have required a certain degree of intelligence was that faced by the second male. Although the second male usually avoided the first male, he did sometimes actively disrupt the first male's copulations. Sometimes, he seemed to disrupt the first male's copulations deliberately by drumming at the pair. Additionally, while

being chased by the first male, the second male occasionally 'circled' back towards the female and courted her while the first male kept moving quickly away from the female. In these two situations, the second male appeared to be performing apparently 'cunning' behaviours in order to gain access to the female. That is, the second male appeared to be acting with intent.

The behaviours of both the first and second male described above could have required intelligence, but they may equally be examples of exceptionally fined-tuned innate responses to specific situations. Many behaviours that appear to require high levels of intelligence can often be the result of less intellectually demanding responses (e.g., the lesson from 'Clever Hans'). Before a behaviour can be labeled as intelligent, other possibilities must first be discredited. Thus, at this stage of research, it appears that the examples described here as 'cunning behaviours' are probably more likely to be examples of elegant innate 'programmes' rather than evidence of intuitive thought.

2.4 Conclusion.

The evidence presented here suggests that *A. antipodiana* do show a limited degree of intelligence in male-male contests in that they are able to assess their opponents' fighting abilities, and that they may try to 'out smart' each other when two males are trying to copulate with the same female. However, in male-male contests, *A. antipodiana* appears to try to reduce the amount of intelligence required to solve the problem (i.e., the problem of deciding a winner) by using internal cues to reduce the need to directly assess the current situation.

3 Behavioural Plasticity Associated with Feeding

A. antipodiana has very versatile foraging behaviours. Firstly, *A. antipodiana* tends to feed by kleptoparasitizing on the webs of larger

orb-weaving spiders. It does this by concentrating on a limited number of host species against which it employs numerous kleptoparasitic techniques. For example, it can feed kleptoparasitically by stealing foodbundles that the host has caught and wrapped by hauling these foodbundles out of the host's web; it can feed directly on small insects caught in the host's web that the host has not responded to; and it can actually move onto the host's web and feed off the same food bundle upon which the host is feeding, without the host responding to its presence. *A.antipodiana* can also feed araneophagically. For example, it is known to feed on moulting host spiders, and *A.antipodiana* sometimes prey on small spiderlings of host spiders encountered in webs.

If problems are predictable, animals can evolve innate responses. An important role of learning is to enable an animal to develop solutions to novel, unpredictable problems. The foraging behaviour of *A.antipodiana* is very complex, with ample opportunities for unpredictable problems to arise. Consequently, foraging behaviours seem to demand learning. To see if learning did play a role in the development of the foraging techniques of *A.antipodiana*, I looked at the means by which *A.antipodiana* acquired both the ability to feed with its most common host *E.pustulosa*, and the ability to catch spiderlings.

3.1 Behavioural plasticity and feeding with the host.

Feeding with the host is arguably one of the main methods by which *A.antipodiana* obtains food (Chapter 7). It is a complex foraging behaviour in which *A.antipodiana* must move down onto the host's web; locate and move directly towards the feeding host; feed undetected right beneath the jaws of the host spider, and perform all of these manoeuvres undetected by the host. As foraging behaviour seemed so dangerous and complex, I wanted to investigate whether it was predominantly learned or innate.

3.1.1 Learnt or innate?

A. antipodiana's ability to feed with the host appears to be largely innately controlled (Chapter 7). Adult *A. antipodiana* which had had no previous experience of feeding with the host, nor even any experience of the host's orb web, were able to move down the orb web to the host and feed with the host. Thus, the ability to feed with the host appears to be largely innately controlled.

Nevertheless, experience did seem to improve the ability of *A. antipodiana* to deal with subtleties associated with feeding with the host, such as solving the problem of reaching awkward food bundles and solving the problem of reducing the likelihood of detection of the host.

3.1.1.1 Problem solving.

Experience improved the ability of *A. antipodiana* to deal with problems associated with locating foodbundles which were difficult to reach. The most common reason why *A. antipodiana* may not be able to reach a foodbundle is because it has approached the host from the 'wrong' side of the web.

To feed with *E. pustulosa*, the best technique is to approach the host from the side of the web opposite to the host and feed on the foodbundle as it sticks through the plane of the web (Fig 1). Evidently, *A. antipodiana* with experience at feeding with the host 'know' that if they approach the host from the same side of the web as the host and can not reach the food, then they need to go around to the other side of the orb web in order to reach the food. Inexperienced *A. antipodiana* do not 'realize' this and repeatedly try to approach the host from the same side of the web as the host. Thus, moving around to the other side of the web appears to be learned with experience.

It is learned because *A. antipodiana* must be relating a response (moving around to the other side of the web) to a problem (not being able

to reach the food) and then remembering the solution to the problem next time it encounters the same problem. Thus, this response appears to be a form of operant conditioning.

3.1.1.2 Detection by the host.

In Chapter 2, I compared the social interactions during kleptoparasitism between female *A.antipodiana* that had experience at feeding with the host and those which were inexperienced at feeding with the host. One of the findings from this study was that inexperienced *A.antipodiana* were more likely to alert the host to their presence than experienced *A.antipodiana*. Thus, *A.antipodiana* appear to improve their ability to move stealthfully on the host's web with experience. By increasing its stealth, *A.antipodiana* not only reduces the risk of predation, but also becomes a more effective thief. At this stage, it is unclear whether the ability to move stealthfully is 'triggered' by exposure to the host and web, or whether it gradually develops over time. Either way, it is another example of *A.antipodiana* subtly modifying its kleptoparasitic behaviour.

3.2 Behavioural plasticity and catching spiderlings.

Catching spiderlings of spiders is arguably a more opportunistic method of obtaining food than feeding with the host. Nevertheless, adult *A.antipodiana* with experience at catching spiderlings were better at catching spiderlings than adults without this experience. However, sub-adult males with no previous experience with spiderlings were as good at catching spiderlings as experienced adult males. Thus, it appears that experienced males did not improve their ability to capture spiderlings, but simply retained the juvenile characteristic which is lost if the males are not exposed to spiderlings.

This form of behavioural plasticity appears to be crudely similar to how critical periods are known to govern behavioural development of some other animals such as the development of vision in cats (Aoki and Siekevitz 1988) and song in certain bird species (e.g. Baptista and Petrinovich 1986). Adult male *A.antipodiana* that had not been exposed as juveniles to spiderlings appear to be unable to develop araneophagy effectively, whereas sub-adult males with no experience are exceptionally good. Another factor that supports the hypothesis of a critical period being involved is that only one aspect, lunging accuracy, actually 'improved' in experienced spiders. Thus, only one behaviour, rather than a whole behavioural sequence, is modified. The control on a single behaviour is presumably a lot simpler than the control of a behavioural sequence, and this may help account for why only the control of lunging ability appears to be governed by a critical period. To trigger maintenance of efficient araneophagy, *A.antipodiana* may simply need to lunge during the critical period. That is, rather than *A.antipodiana* improving their ability to capture spiderlings with practise, they may simply be good or poor depending on whether they lunged as sub-adults.

This has important implications for understanding the foraging behaviour of *A.antipodiana*. It appears that a single change in a behavioural sequence results in a large behavioural change in foraging behaviour. It appears that by simply improving lunging accuracy, a whole new area of foraging becomes available to *A.antipodiana*.

Additionally, this major development does not appear to be the result of an advanced form of learning in the sense discussed in Chapter 8, but may be evidence of the existence of a 'critical period' in the development of foraging behaviour in *A.antipodiana*. Through the critical period, behavioural modification appears to be simply the result of appropriate exposure at the right time. Consequently, the means by which lunging ability is improved in *A.antipodiana* may arguably be, at most, a simple

form of learning.

3.3 Comparison between behavioural plasticity in kleptoparasitism and araneophagy.

Experience with an opportunistic feeding method (catching spiderlings) appears to govern a major behavioural change. Apparently, a relatively simple method is involved. The behavioural change, improved ability to catch spiderlings, has important implications for understanding the feeding behaviour of *A.antipodiana* - it enables *A.antipodiana* to effectively exploit another food source (spiderlings) should they be plentiful. Thus, it enables *A.antipodiana* to adjust its behaviour to current environmental conditions. However, the method by which this exploitation is probably achieved (use of a critical period) does not appear to be very advanced cognitively. The fact that *A.antipodiana* used such a simple method for such a major change in behaviour is very revealing, and seems to support the view that learning in *A.antipodiana* is heavily constrained. That is, whenever possible, *A.antipodiana* appears to use the method that requires the least amount of learning and intelligence to solve the problem.

In contrast, behavioural plasticity associated with *A.antipodiana's* most commonly used feeding method (kleptoparasitism) only resulted in minor behavioural adjustments. These adjustments, however, involved more advanced methods of behavioural modification (problem solving). Although they appeared only minor, these behavioural adjustments (learning to change sides and avoiding detection by the host) were very important as they allowed more effective exploitation of the host. As *A.antipodiana* in Australia is known to exploit other host species (Elgar 1989), this flexibility may be especially pertinent for fine tuning of behaviour to effective exploitation of different hosts.

In summary, the feeding behaviour of *A.antipodiana* was highly versatile; however, this versatility appears to be largely innately determined, as *A.antipodiana* were capable of performing both kleptoparasitic and araneophagic behaviours innately. Nevertheless, *A.antipodiana* was able to adjust its foraging behaviour in response to both the host and to spider-prey abundance. Thus *A.antipodiana* appeared to modify its foraging behaviour by using the simplest methods possible. In addition it appeared to be only capable of modifying small parts of its behavioural repertoire. These responses seemed to reflect the degree to which learning in *A.antipodiana* is heavily constrained and narrowly channeled.

CONCLUSION

In Chapter 8, I defined intelligence as the ability to manipulate information, ideas or behaviours in order to solve problems. I argued that intelligence is not an absolute, which animals either do or do not have, but rather that it is something that varies in degree between animals. Intelligence, I suggested, varies between animals in both the number of situations in which it can be applied, and in the complexity which can be achieved. Thus we may envisage an animal's intelligence falling anywhere within a 'two-dimensional area'.

The intelligence of *A.antipodiana* appears to be limited. Nevertheless *A.antipodiana* appears to have been able to overcome these limitations very effectively by using four methods. Firstly, *A.antipodiana* simplifies the situation as much as possible by ignoring some of the variability. For example, in social situations, *A.antipodiana* appears to recognize only a few categories of conspecifics, rather than recognize conspecifics as individuals. Consequently the social groups of *A.antipodiana* are not characterized by complicating factors such as aggressive orders or dominance hierarchies.

Secondly, *A. antipodiana* largely ignores current situations and instead bases much of its behavioural decisions on its internal conditions. For example, in male-male conflicts, males respond to their opponents largely according to their own size, level of hunger, amount of previous contesting, or past experience of winning or losing; rather than to the characteristics of their opponents. Likewise, in social interactions *A. antipodiana* is more inclined to be aggressive towards conspecifics if it itself is foraging, and less inclined if it is feeding with the host.

When the situation can not be simplified, *A. antipodiana* adopts a third response which is to use the simplest method possible for adjusting its behaviour. For example, *A. antipodiana's* ability to develop araneophagic skills appears to be governed by a critical period. Thus rather than developing araneophagic skills through trial and error with practice, the ability appears to be simply 'switched on' if required.

The fourth means by which *A. antipodiana* compensates for limited intelligence is to be very selective in the areas in which it does use learning. For example, *A. antipodiana* seems to use problem solving techniques in order to feed with the host; it apparently learns to move more stealthfully on the host's web; and during male-male conflicts it is capable of assessment. There is even evidence that *A. antipodiana* may behave with intent when males are competing for opportunities to copulate.

An important role of learning and intelligence is to enable an animal develop solutions to novel, unpredictable problems. The peaks of cognitive activity described above appear to be channeled into areas where *A. antipodiana* probably cannot 'predict' an appropriate response. *A. antipodiana* cannot predict the idiosyncrasies of its chosen host, nor is it likely to be able to predict the characteristics of its opponents in male-male contests.

In conclusion, the intelligence of *A.antipodiana* appears to be severely limited. However, despite these limitations, *A.antipodiana* thrives in a complex, variable environment. It is able to do this by: apparently largely ignoring much of the variability, using its internal conditions to determine its behaviour, and by modifying its behaviour with the method which involves the least amount of cognition possible. These responses greatly reduce the amount of learning necessary. Consequently, *A.antipodiana* has apparently channeled what learning it has to very restricted but very poignant areas of its behaviour. By responding in this manner, *A.antipodiana*, with what it has, is able to respond very effectively to the variable conditions it encounters when it is socializing, mating, fighting, and feeding.

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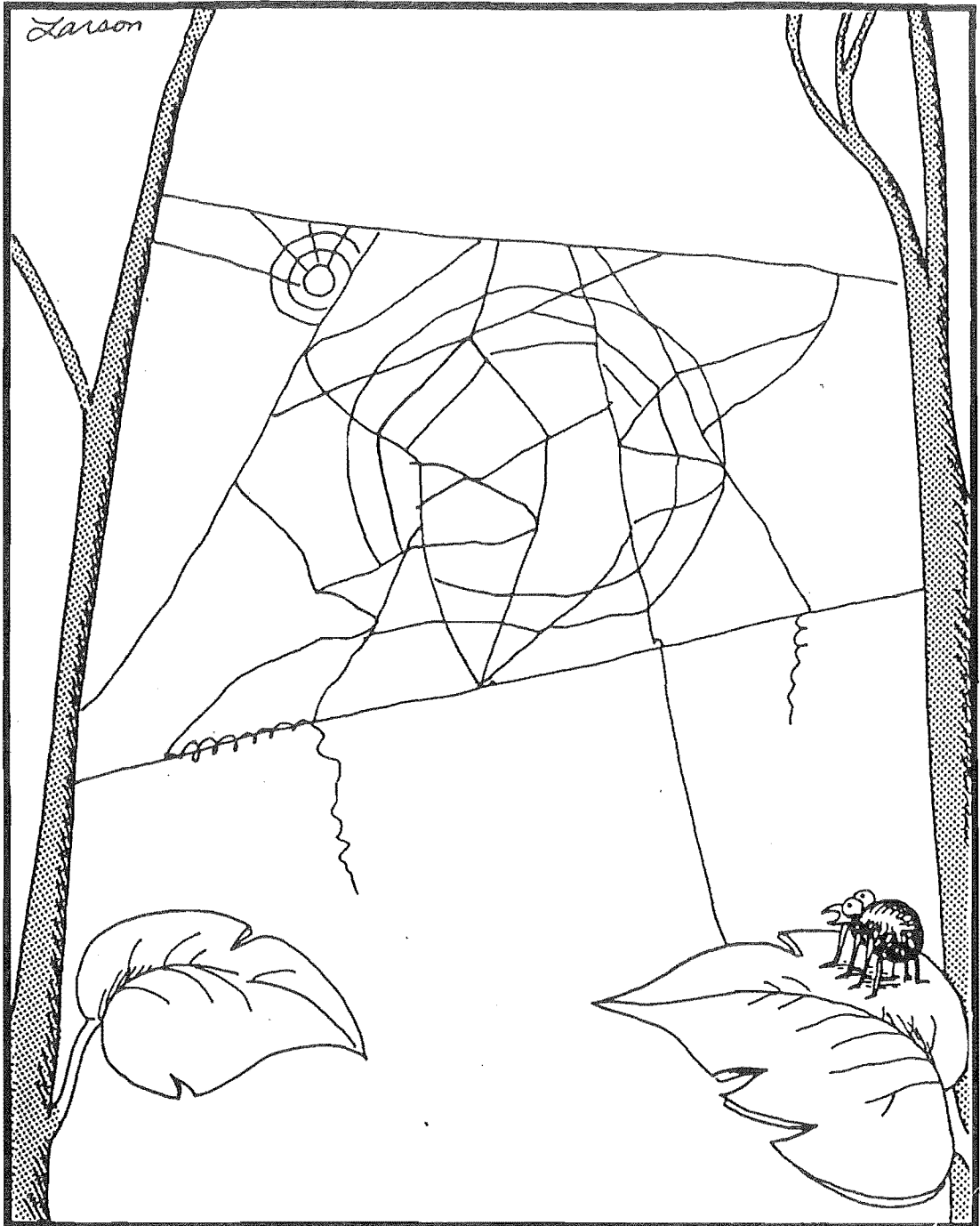
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"Whoa! . . . That CAN'T be right!"