Effects of water depth on choice of spatially separated prey by *Notonecta glauca* L.

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**Summary.** In laboratory experiments, the predator, *Notonecta glauca* L., was exposed to varying densities of surface-dwelling culicine mosquito larvae and the bottom-inhabiting isopod, *Asellus aquaticus* L., in either shallow or deep water at 20 °C. At this temperature *N. glauca* spends most of the time at the water’s surface, so, by changing water depth the accessibility of *Asellus* to the predator was manipulated relative to a consistent *Culex* presence.

All *N. glauca* spent more time submerged in shallow (75 mm) than in deep (275 mm) water but submergence times were independent of exposure to different prey combinations. Mature females made more descents and remained submerged longer than males.

All *N. glauca* captured more *Asellus* in shallow than in deep water but males and newly-moulted females captured *Culex* predominantly, in all treatments, regardless of water depth or prey availability. Mature females captured mostly *Asellus* in shallow water and *Culex* in deep water. When presented with small rather than large *Asellus*, mature females spent an equivalent amount of time submerged as in the large *Asellus* treatments and ate the same number of *Asellus* but more *Culex*.

By foraging on *Culex* larvae, male and newly moulted female *N. glauca* maximise their rate of energy intake. In contrast, mature females may actively select *Asellus* to optimise something other than energy (e.g. specific nutrients). Alternatively their predation on *Asellus* may be simply a consequence of a high encounter rate with this prey type, reflecting habitat use determined by factors that do not concern prey capture directly.

**Introduction**

Prey choice by the aquatic hemipteran, *N. glauca*, was investigated with respect to the availability of two prey types, one of which occurs at the water’s surface, the other on the underlying substrate. Usually a predator’s choice of prey has been considered separately from its habitat selection. Optimal prey choice models generally assume that a predator selects prey from a fine-grained assemblage. The prey items are searched for simultaneously and are randomly distributed and encountered. Pyke et al. (1977), cite nine independent derivations of what is essentially the same prey choice model, which predicts that a predator should consume or reject a prey type on the basis of the availability of more profitable prey. In many tests of prey choice the prey types have been different sizes or stages of a single prey species which occupy a single subhabitat (e.g. Werner and Hall 1974; Goss-Custard 1977), or they have been presented within a simplified environment, which artificially increases their proximity to one another (e.g. Jaeger and Barnard 1981). Some of the results of such experiments concur with optimal foraging predictions (see Pyke et al. 1977; Krebs 1978), although others do not (e.g. Emlen and Emlen 1975).

The assumptions of these general optimal prey choice models are not appropriate for certain natural conditions. For instance, where the prey types of polyphagous predators comprise different species which occupy different subhabitats, their spatial separation prevents their simultaneous exposure to the predator which must therefore hunt for each type independently. Under these circumstances prey choice becomes a matter of patch choice (Hassell and Southwood 1978).

Optimal patch use models predict that predators will concentrate their foraging activity in areas of highest profitability, progressively adding in patches of lower return depending on the availability of more profitable patches and as depletion within patches occurs (Royama 1970; Charnov 1976; Cook and Hubbard 1977). Many practical tests of patch use support these predictions (Hassell and May 1974; Hubbard and Cook 1978), although almost all have examined the predator's response to different density patches of a single prey type only. Provided the currency for optimisation has been correctly identified and is sufficiently basic, patch use theory should also be applicable to patches of mixed prey types as well as to prey segregated between patches.

There have been few investigations of prey choice between spatially separated prey but Murdoch et al. (1975) examined this in a three-dimensional aquatic system using guppies presented with varying ratios of wingless *Drosophila* floating on the water’s surface and tubificid worms on the aquarium floor. Certain of the fish showed strong “switching” behaviour (Murdoch 1969), spending a greater proportion of time in the area occupied by the more abundant prey and attacking this prey type supraproportionately. Similarly, Werner and Mittleback (1981) report seasonal habitat shifts by bluegill sunfish between areas of vegetation, sediment and open water. They found that the
fish switched habitats, and consequently diets, when the profitability of one site fell below that of another. In both these studies prey availability appeared to determine the choice of subhabitat and prey selected by the fish. However, other studies have indicated that prey characteristics such as availability or profitability are not the sole, or necessarily the primary, determinants of patch selection. Instead, a variety of biotic and abiotic factors, including the risk of predation to the predator itself (Milinski and Heller 1978; Sih 1980) and aspects of the physical environment (Cockrell 1984) may act together to determine patch use. Sometimes one or more of these factors may be more important determinants of patch choice than are prey density or profitability. Such factors will affect the spatial coincidence and hence the encounter rates between the predator and separated prey types (Griffiths 1969; Royama 1970). Consequently, in some instances, prey selection may be an effect rather than a cause of patch choice.

One environmental factor that may influence prey choice by *Notonecta* is water depth. Under natural conditions *N. glauca* exploits a wide range of prey types which occupy a variety of subhabitats within still water bodies that include shallow ponds and ditches as well as deep canals and lakes (Southwood and Leston 1959). In this investigation, the availability of the two spatially separated prey types was manipulated, not only by varying the density and size of prey presented, but also by altering their relative accessibility to the predator, through changing water depth.

**Method**

The investigation comprised a series of related experiments that were performed in a tank, 18.5 cm x 29 cm, filled to a depth of 75 mm, or 275 mm with dechlorinated water at 20°C. The predators were field collected *Notonecta glauca* that were acclimatized for a minimum of two weeks to laboratory conditions (16 h light/8 h dark) and were maintained on a mixed diet of field-collected material. A single predator starved for 24h prior to experimentation was used per replicate, with different predators comprising each treatment. The prey were *Asellus aquaticus*, either 7-8 mm or 3-4 mm in length, and fourth instar *Culex pipiens molestus* Forshall larvae. The *Asellus* occupied the tank floor, whilst *Culex* larvae adopt a surface position for 95% of the time at this temperature (Cockrell 1984). Where experiments were continuously observed, the time the predator allocated to the top, middle or bottom regions of the tank (equal divisions) was recorded over a three hour period, together with the success and failure of attacks.

In all experiments, a green dowel rod, 4 mm diameter, was suspended vertically in the centre of the tank which enabled the predator to perch at any level within the water column. Experiments (i), (ii) and (iii) below, were performed between January and March using adults of five months or more, whilst (iv) was performed in September and October using newly moulted *N. glauca*. Eight replicates were performed per treatment in all experiments except (ii) where there were five replicates per treatment.

(i) **Water depth and prey abundance**

Continuous observations were made of *N. glauca* exposed to eight *Asellus* with eight *Culex*, and to twenty-four of one prey type with eight of the other, in shallow (75 mm) and deep (275 mm) water.

| Table 1. Prey combinations used in experiments lasting six hours (A = Asellus, C = Culex) |
|---------------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
|                                | 8A/8C           | 24A/8C          | 8A/24C          | 24A/0C          | 56A/8C          | 8A/56C          |
| Males/                          | +               | +               | +               | +               | +               | +               |
| shallow                         |                 |                 |                 |                 |                 |                 |
| Males/                          | +               |                 |                 | +               |                 | +               |
| deep                            |                 |                 |                 |                 |                 |                 |
| Females/                        | +               | +               | +               |                 |                 | +               |
| shallow                         |                 |                 |                 |                 |                 |                 |
| Females/                        | +               | +               |                 | +               |                 | +               |
| deep                            |                 |                 |                 |                 |                 |                 |

(ii) **Extended experiments**

Some of the three hour experiments, together with some more extreme combinations of the two prey types (Table 1) were run for six hours, after which the number of each prey type eaten was scored.

(iii) **Prey size**

Continual observations were made of female *N. glauca* exposed to either eight or twenty-four small (3-4 mm) *Asellus*, with eight fourth instar *Culex* larvae (as before) in shallow water.

(iv) **Seasonal differences**

In September and October, observations were made of predation by newly moulted *N. glauca* on twenty-four *Asellus* (7-8 mm) with eight *Culex*, and eight of each prey type, in shallow water.

**Results**

(i) **Water depth and prey abundance**

*N. glauca* occupied the middle region of the tank for less than 5% of the total time in all treatments. Instead, predators spent the majority of time at the water's surface at both depths but spent significantly more time submerged in shallow than in deep water (Fig. 1a; $F_{1,84}=48.56, P<0.001$). This was a consequence of an increase in the number (Fig. 1b, $F_{1,84}=27.01, P<0.001$) and duration (Fig. 1c, Mann-Whitney U test, $z=2.06, P<0.05$) of descents made in shallow water. The different prey combinations had no significant effect on total submergence time, or the number or duration of descents. Although both males and females behaved in this way, females spent more time submerged, making more descents of longer duration than males. As a result females spent most of the non-feeding period submerged in shallow water.

All predators attacked and ate more *Asellus* in shallow than in deep water (Fig. 2; $F_{1,84}=37.4, P<0.001$) with females consistently capturing more *Asellus* than males at an equivalent water depth ($F_{1,84}=48.9, P<0.001$). Overall there was increased predation on *Asellus* at the higher *Asellus* density ($F_{2,84}=4.01, P<0.05$).

Females ate significantly more *Culex* in deep than in shallow water (Fig. 2), but water depth did not significantly affect the number of *Culex* eaten by males ($F_{1,42}=0.17$).