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ECOLOGICAL AND BEHAVIOURAL CHARACTERISTICS OF *GEOPHILUS EASONI* ARTHUR ET AL. AND *G. CARPOPHAGUS* LEACH

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INTRODUCTION

Eason (1979) described 'long' and 'short' forms of *Geophilus carpophagus* Leach based on (a) different maximum body lengths, (b) non-overlapping distributions of segment number and (c) a difference in habitat. Eason's specimens of the short (or typical) form male had 45-49 trunk segments, while his sole long form male had 53. The equivalent numbers for Eason's females were 47-53 (short) and 55-57 (long). Eason regarded the long form as a resident of urban and domestic localities, which as a generalization is incorrect (see below). He postulated that the difference in segment number between the two forms was due to an environmental factor - perhaps temperature - having a direct effect on the phenotype. However, other possibilities remained open, and Lewis (1985) suggested that the two forms might be distinct species. The recent confirmation of this (Arthur *et al.* 2001) was based on both morphological and molecular evidence. The former included not only segment number and body length, but also pigmentation, number of coxal pores, and number of teeth on the mid-piece of the labrum. The latter included six metabolic enzymes (out of nine studied) that were diagnostic in that the populations of *G. easoni* and *G. carpophagus* studied were fixed for different alleles. Because Leach's (1815) original description relates to three type specimens in the Natural History Museum that are 'long' (55/57 trunk segments), this form, which is by far the less common of the two, is *G. carpophagus*, while the common 'short' form is *G. easoni*.

Here, we add some information on ecological and behavioural differences between the two species. This information is less clear-cut than its morphological or molecular counterpart, and should not be regarded as diagnostic on its own. However, it should be particularly useful to field workers, in conjunction with those morphological differences that can readily be observed in the field - principally body length and pigmentation. (*G. carpophagus* is usually greenish grey or brownish grey in contrast to *G. easoni*'s typical tan or chestnut colour.) Ironically, we mainly focus here on *G. carpophagus*, as most existing information on distribution and ecology (e.g. Eason 1964, Barber & Keay 1988) is now seen to relate to *G. easoni*.

HABITATS AND GENERAL ECOLOGY

Leach's (1815) original specimens of *G. carpophagus* were collected from somewhere in Devon or Cornwall, but neither the exact locality nor the habitat were given. Subsequently, specimens of this species have been collected from at least ten British localities (see Table 1). These include the two sampled by Eason (1979), others sampled by various workers over the last two decades, and further sites described for

the first time in the present paper. There are three themes running through this list of sites.

1. Many sites are coastal. *G. carpophagus* is often found on cliffs and other rocky areas within about 100m of the high tide mark. It is emphatically not an intertidal species, like *Hydroschendyla submarina*, nor even a littoral fringe species, like *Strigamia maritima* (Lewis 1962) which is largely confined to a narrow band around the high tide mark. Nevertheless it has a clear association with the coast. Individuals living in these coastal cliff/rock sites are typically found at heights ranging from 1-3 metres above the base of the cliff. Of course, in the case of tall cliffs they may also be found higher up, but this has not been investigated. No inland sites inhabited by *G. carpophagus* have yet been found north of Gloucestershire.

2. In the non-coastal sites, the association with climbing behaviour and living 1m or more above the ground remains. These inland sites all involve rocks, walls, buildings or trees (including elm, pine and yew). Eason's (1979) view that his 'long form', i.e. what we now recognize as *G. carpophagus* sunsu stricto, lived in urban and domestic localities, was an overgeneralization based on two collection sites, one being his own farm outbuildings in Gloucestershire, the other a towpath by the Thames in Mortlake, Greater London. The 'domestic' and 'urban' labels can now be seen to emphasize the wrong aspect of the sites, especially in the latter case, where the specimens were found "under elm bark" (height not specified). Occupation of such a microhabitat clearly involves climbing behaviour. Even in the case of Eason's Gloucestershire farm, where the individuals collected were from the ground floor of the buildings, Eason describes one individual as "presumably having come up the waste pipe" - i.e. again a link with climbing behaviour. Also, we have noticed a peculiar characteristic of *G. carpophagus* that may well be associated with its tendency to climb. Individuals crawling over one's hand are very difficult to shake off. They often have to be 'peeled' off, and their adhesive power can be clearly felt while doing so. In contrast, individuals of *G. easoni*, like those of other British geophilomorph species, can be shaken off with ease.

3. All sites where *G. carpophagus* has been found, both coastal and inland, tend to be much drier than the sites used by *G. easoni*, the latter typically being found both in woodland leaf litter and in semi-decayed vegetation under stones in moorland areas. In fact, the *G. carpophagus* sites that we have sampled seem drier than those of British geophilomorphs generally. Admittedly this is based on subjective assessment of field sites, and needs to be confirmed by measurement of relative humidities in the microhabitats themselves. Nevertheless, the characteristic dryness of most *G. carpophagus* sites is so striking that we are confident that objective confirmation will follow. It is possible that there is a link between this dryness and the reduced number and size of coxal pores of *G. carpophagus* compared to *G. easoni*. However, this is merely a hypothesis, especially given that the function of the coxal pores remains debatable (see Littlewood 1991 and references therein) and the degree to which they contribute to water loss remains unquantified.

TABLE 1

SAMPLE SITES IN GREAT BRITAIN FROM WHICH SPECIMENS OF *GEOPHILUS CARPOPHAGUS* HAVE BEEN COLLECTED

Site	Habitat description	Source
Mortlake, Greater London	Under elm bark on the Thames towpath	Eason (1979)
Bourton Far Hill, Gloucs.	Farmhouse and outbuildings	Eason (1979)
Horton, Gower Peninsula, West Glamorgan	Trunks of pine trees; garden wall	Blower (1987)
St. Margaret's at Cliffe, Dover	Inside houses, including upstairs rooms; on apple tree; under bark	Lewis (1985)
Taunton and Williton, Somerset	Inside farm and school buildings	Lewis (1989)
Gunwalloe, Cornwall	Coastal cliffs, well above the high tide mark	This paper
Moreton and Bobbingworth, Essex	Under bark of yew and Scots pine, in churchyards	This paper
Kincraig Cliffs, Fife	Coastal cliffs, well above high tide mark	This paper[1]
Isle of May, Fife	Rocky, disturbed area	This paper[1]
Inchcolm Island, Fife	Coastal cliffs, well above high tide mark	This paper[1]

[1]Collected by Gordon Corbet

BEHAVIOUR IN THE LABORATORY

Over the last two years, we have kept cultures of both species in the laboratory. These have been collected from several sites, and have been maintained for varying periods. The largest and longest-surviving laboratory cultures were established from collections at Doddington, Northumberland (*G. easoni*) and Kincraig, Fife (*G. carpophagus*). These cultures consist mostly of adults, but also a few juveniles. Females of both species have produced broods (typically of 10-20 eggs) in the laboratory, which have often then been deserted or eaten, possibly due to disturbance. However, one *G. carpophagus* brood hatched, producing live young. We report on two aspects of behaviour below: brooding and defence. In the former case, the

observations were accumulated in a casual way over long periods; in the latter case, they are quantified and result from a single experiment.

Aspects of brooding behaviour

We have noticed two differences in brooding behaviour between the two species. These all relate to adult females kept in transparent plastic boxes (approx. 14 x 8 x 5 cm) containing only moistened kitchen roll and a food source (*Drosophila*). First, *G. carpophagus* females have a distinct tendency to rip up the kitchen roll in an apparent attempt to dig a brood cavity. The broods are then produced in the ripped-up area. Second, they are much more persistent in their attempts to protect their eggs than either *G. easoni* or other species that we have observed in this respect, such as *Strigamia maritima.* They are unique in that mothers that have been deliberately disturbed and have left their brood will often return to it and coil around it again. We have never observed this behaviour in any other species.

Aspects of defensive behaviour

We performed a replicated experiment designed to simulate attempted attack by a predator (e.g. a bird) as follows. A centipede was placed on a tray and left to settle for 30 seconds. It was then tapped on the head with a paintbrush every 30 seconds for 10 repetitions. The response was classified as follows. (a) Recoil (= negative) response, given values of -0.5 (pause), -1.0 (drew back front half of body), -1.5 (drew back entire body) and -2.0 (drew back and changed direction). (b) Neutral (= zero) response. (c) Aggressive (= positive) response, given values of +1.0 (head rears up bearing poison claws) and +2.0 (as before, but posterior end rears up simultaneously). Each individual centipede was given a mean score. Various sample sizes were used, reflecting availability of each species, and the whole experiment was repeated a second time. We included *Haplophilus subterraneus* and *Strigamia maritima* as well as the two *Geophilus* species. It is worth noting that *H. subterraneus* is an inland species, *S. maritima* a coastal one.

The results of this experiment are shown in Figure 1. Clearly, there are repeatable differences between the species, with the two inland species exhibiting aggressive responses, the two coastal (or predominantly coastal) ones exhibiting recoil responses. It is particularly interesting that the two *Geophilus* species are so different to each other, and that each is rather similar to a more distantly-related species with which it shares a broad habitat type. One possible reason for this overall pattern may be convergent evolution of behaviour in response to different types or levels of predation between coastal and inland habitats.

FUTURE STUDIES

The discovery that *G. easoni* and *G. carpophagus* are distinct species raises many questions. As already noted (Arthur *et al.* 2001), one of the main tasks ahead is to determine the taxomonic status of populations recorded previously as *G. carpophagus* from mainland Europe, North Africa and offshore islands such as the Canaries. However, even within the British Isles many questions remain. Both species are found from southern England to at least central Scotland. But how far north do they

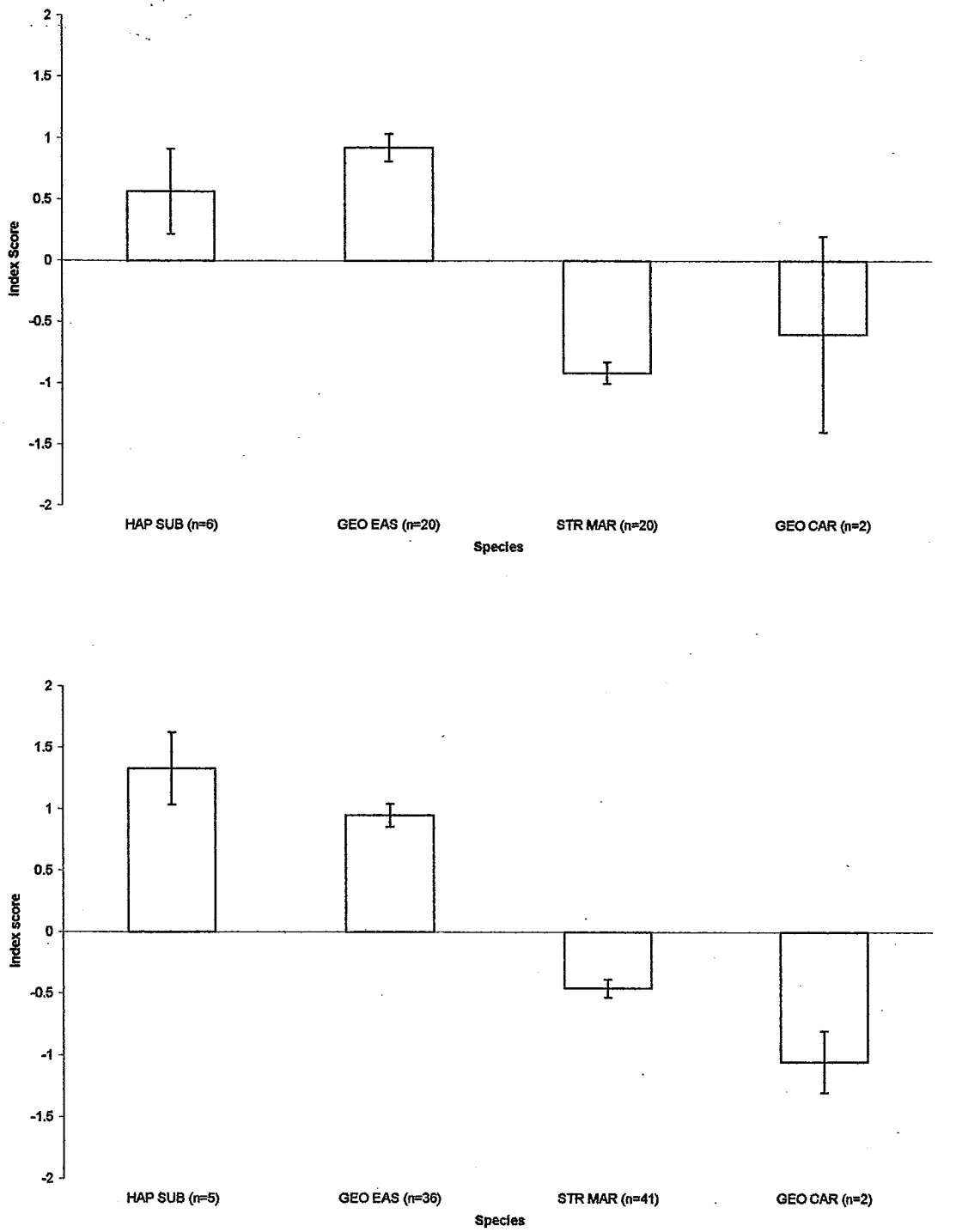

FIGURE 1

Results of experiment on defensive behaviour. For explanation of index score, see text. Bars are standard errors. Top panel - original experiment; bottom panel - repeat experiment conducted two weeks later to test for consistency of results. Sample sizes of *H. subterraneus* and *G. carpophagus* are too small to allow signficance testing, but *G. easoni* and *S. maritima* differ at the $p<0.001$ level (χ^2 on the ratio of positive to negative index scores).

go? There are distributional records for northern Scotland (Barber & Keay 1988), but it is not clear whether these represent *G. easoni*, *G. carpophagus*, or both. Also, the situation in Ireland will need to be clarified. There are very few records for Ireland, and most of these are rather old (pre-1939; Barber & Keay 1988).

Ecological information is only meaningful against a background of known taxonomy, so the first task is to re-check museum specimens where possible, to re-sample areas from which previously-collected specimens are no longer available, and to sample new areas. This way, a picture of the distribution of the two species will be gradually built up. It will be important to monitor several characters rather than just the primary one of segment number, especially in Irish and European samples. The reason for this is that although the distributions of segment number for British *G. easoni* and *G. carpophagus* are virtually non-overlapping (Arthur *et al* 2001), the situation may well be different elsewhere. Latitudinal clines in geophilomorph segment number have been demonstrated in other species (Kettle & Arthur 2000, Arthur & Kettle 2001), with segment number increasing in more southerly locations; and "*G.carpophagus*" specimens from the Canaries have more segments than either British species (Arthur & Kettle 2001). Is a 61-segment female from the Canaries a very elongated *G. easoni*, a slightly elongated *G. carpophagus* or another species altogether? The answer is not yet clear.

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