Manipulation of a mollusc by a trophically transmitted parasite: convergent evolution or phylogenetic inheritance?

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SUMMARY

We investigated the influence of infection by the trematode *Curtuteria australis* on the burrowing behaviour of its intermediate host, the bivalve *Austrovenus stutchburyi*. Laboratory experiments and field observations revealed that cockles, unable to bury completely or even partially under the sediment, have a reduced foot length compared with buried individuals. The ability to bury proved to be highly repeatable in field experiments: cockles found at the surface and transplanted to an experimental area did not bury themselves, and cockles found buried stayed buried when relocated. All metacercariae of *C. australis* were found strictly in the foot and for each of 3 samples collected in different sites, there was a negative and significant relationship between the relative length of the foot and the parasite load. A predation test conducted under natural conditions indicated that cockles with the stunted foot and the altered behaviour are significantly more susceptible to predation by aquatic birds than other cockles. Given that the definitive host of *C. australis* is an oystercatcher, we first discuss our results in the context of transmission strategy. Comparisons with other studies on more or less related trematode species parasitic in bivalves and evolving under similar constraints for their transmission, shed light on the origin of this adaptation in *C. australis*.

Key words: parasite, host behaviour, trematode, phylogeny, *Curtuteria australis*, *Austrovenus stutchburyi*.

INTRODUCTION

Many parasites with complex life-cycles are able to alter host phenotype in a way that favours the continuation of their life-cycle. Behavioural changes have been particularly well documented in a variety of host–parasite systems. For example, many trophically transmitted parasites increase the vulnerability of the intermediate host to the predatory definitive hosts (Holmes & Bethel, 1972; Helluy, 1984; Moore, 1984; Hechtel, Johnson & Juliano, 1993). Fungal parasites can make their insect hosts die perched in an optimal position for the dispersal of fungal spores by the wind (Maitland, 1994). Mermithid nematodes can make males in insects behave like females when parasitic transmission is dependent on a female-specific behaviour (Vance, 1996). Some digeneans can make their mollusc intermediate host migrate toward ideal sites for the release of cercariae (Curtis, 1987). Although the adaptive value of these changes has not been always demonstrated (Poulin, 1995), many are undoubtedly true adaptations for transmission.

Recently, there has been a growing interest in understanding the origin of similar behavioural changes induced by different parasite species. It seems likely that many parasite species evolve under similar selective pressures because they exploit the same host species in the same sequence, or different host species but in a similar context. Convergent evolution, however, has to be examined properly within a phylogenetic context since the ability to modify host behaviour among related parasites can be inherited from a common ancestor (Poulin, 1995). When similar behavioural changes are induced by phylogenetically unrelated parasites experiencing similar selective pressures, convergence is a reasonable explanation since the same manipulation of host behaviour could have arisen independently in different parasite lineages. For instance, there are suggestions that mermithids (Nematoda) and hairworms (Nematomorpha) are both able to alter the behaviour of their insect host, making them enter water where the adult worm must emerge (Poinar, 1991*a*, *b*; Maeyama, Terayama & Matsumoto, 1994). Both *Polymorphus minutus* (Acanthocephala) (Holmes & Bethel, 1972) and *Microphallus papillorobustus* (Trematoda) (Helluy, 1984) induce in gammarids a photophilic behaviour that renders crustaceans more vulnerable to predation by aquatic birds (definitive hosts).

Another situation where convergence is a likely scenario is when host behavioural alterations lead to the same function but are derived from different proximal mechanisms (Poulin, 1995). For instance, among European trematode species, at least 3 specific mechanisms have been hypothesized to increase the

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vulnerability of bivalve intermediate hosts to predation by oystercatchers (definitive host): (i) *Meiogymnophallus fossarum* (Gymnophallidae) encysts in the mantle of *Venerupis aurea* and infected molluscs reverse their position in the mud and remain closer to the surface than uninfected individuals (Bartoli, 1974), (ii) cercariae of *Parvatrema affinis* (Gymnophallidae) encyst everywhere inside the bivalve *Macoma balthica*; infected molluscs are still able to burrow but they indicate their location to predators by making noticeable crawling tracks on the surface of tidal flats (Swennen, 1969, but see Mouritsen, 1997) and (iii) cercariae of *Himasthla elongata* (Echinostomatidae; Himasthlinae) encyst in the foot of *Cardium edule* and infected molluscs have then a reduced ability to burrow (Laukner, 1984). In these examples, manipulation of the host behaviour is thus derived from different proximal mechanisms and is consequently unlikely to be an ancestral legacy.

The New Zealand trematode *Curtuteria australis* (Echinostomatidae, Himasthlinae) is also trophically transmitted to oystercatchers from bivalve intermediate hosts (the cockle *Austrovenus stutchburyi*) (Allison, 1979). We designed the present study to determine whether or not *C. australis* is also able to manipulate the behaviour of bivalves in order to facilitate its transmission. Because *C. australis* is related to *H. elongata*, and because Laukner (1984) did not verify the adaptiveness of the alteration caused by *H. elongata* in its cockle host, our system can provide useful data for comparative purposes. We observed infected bivalves in the laboratory and in the field, and we conducted a predation test in natural conditions. The results are discussed in relation to the phylogenetic relationships among trematodes parasitic in bivalves and known to alter host behaviour.

MATERIALS AND METHODS

Laboratory experiment

We first studied the behaviour of infected *A. stutchburyi* in the laboratory using individuals for which we had no information regarding position (i.e. either buried or at the surface) in nature. These cockles (sample S1, $n = 36$) came from a natural lagoon (Blueskin Bay, north of Dunedin, South Island of New Zealand). We studied behaviour in plastic transparent glasses (diameter: 7 cm, height: 15 cm) containing 10 cm of natural sediment (mixture of sand and mud). We placed half of the cockles at the surface of the sediment and the other half a few centimetres under the sediment (1 cockle/glass). Then, all the glasses were placed together in a large aquarium filled with constantly aerated sea water (15 °C, 38‰) and under natural photoperiod (10 h light: 14 h dark). After 24 h, we classified the position of cockles as follows: 'inconspicuous' when individuals were completely invisible from the surface, and 'conspicuous' when individuals were either lying at the surface or only partially buried. We repeated the same experiment but individuals previously placed at the surface were this time placed under the sediment, and vice versa. After this, all cockles were sacrificed and we measured the maximum length of the shell to the nearest mm. The foot was straightened without stretching and also measured to the nearest mm. Cockles were then removed from the shell and placed in a digestive solution (6 g pepsin and 7 ml of concentrated HCl in 1000 ml of distilled water (Lepitzki *et al.* 1994)) during 24 h before being dissected. We then determined the exact parasite load of *C. australis* of each individual by counting all metacercarial cysts (transparent cysts with a diameter of 230 μm (Allison, 1979)).

Field study

The aim of this study was to quantify the relationship between the position of cockles in nature (and its repeatability) and their parasite load. We first collected 2 samples (S2 and S3) in 2 localities (Company Bay and Waipuna Bay) on opposite sides of the Otago harbour, near Dunedin, during May and June 1997, respectively. During the sampling, we checked for the presence of crawling tracks and as before we classified individuals sampled as either 'conspicuous' or 'inconspicuous'. All the cockles were then sacrificed, measured to the nearest mm (shell and foot) and dissected to determine their exact parasite load following digestion.

To measure the repeatability of the behaviour in the field, we collected another sample (S4, $n = 100$) of cockles either fully buried ($n = 50$) or lying entirely exposed at the surface ($n = 50$) of the sediment in the same sampling area as for S2. The mean shell length of buried and surface cockles was not significantly different (unpaired t-test, $t = 0{\cdot}05$, D.F. $= 198$, $P = 0{\cdot}96$). In the laboratory, we made 1 distinctive symbol on the shell of each cockle using a water-resistant pen. These cockles were returned to the field and placed in a delimited area (10×5 m) at low tide. After 72 h (i.e. 3 tide cycles), we recorded the position of each individual using the same criteria as during the sampling.

Predation experiment

We conducted a predation experiment under natural conditions using cockles previously found buried under ($n = 102$), or at the surface ($n = 102$) of the sediment in the field. The mean shell length of these 2 groups was not significantly different (t-test, $t = 0{\cdot}2$, D.F. $= 202$, $P = 0{\cdot}84$). Because cockles in the field may be displaced by currents or may be difficult

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to find again under the sediment, we attached them to iron stakes using a transparent string (20 cm) with a small piece of brown tissue (1 cm × 0·5 cm) glued on the shell with Superglue. On each of the 51 stakes, we attached 2 cockles previously found at the surface and 2 cockles previously found under the sediment. For cockles found at the surface, we darkened the part of the string closest to the stake over 2 cm with a water-resistant pen, allowing us to discriminate at any time the 2 categories of cockles on each stake. This darkened part was under the sediment during the entire experiment and had thus no chance to influence predation. Stakes were planted 1 m apart along a transect running parallel to the low water mark; stakes were not visible from above. We started this experiment in August (winter) and we stopped it 7 weeks later because oystercatchers became less abundant on the coast during their breeding season. We checked predation every week by examining each stake at low tide. In a few cases cockles were found unglued and still alive near the string. In our test, we concluded that predation had occurred only when the shell was broken with at least a fragment of shell still attached to the string. We do not know fish species able to break the shell of cockles in this way, while previous observations by us of foraging oystercatchers in Waipuna Bay revealed that the shell of predated cockles is frequently broken.

All statistical tests were performed following Sokal & Rohlf (1981) and Siegel & Castellan (1988). All tests were 2-tailed. Throughout the paper values given are mean ± S.D. Results were considered significant at the 5 % level.

RESULTS

Laboratory experiment

None of the 36 (S1) cockles placed under the sediment became conspicuous after 24 h. However, when cockles were placed lying at the surface, 30 buried themselves completely and became 'inconspicuous', while 6 remained partially at the surface and were thus 'conspicuous'. The length of the shell was not significantly different between these conspicuous and inconspicuous cockles (Table 1, unpaired t-test, $t = 1{\cdot}82$, D.F. = 34, $P = 0{\cdot}08$). However, the relative foot length (i.e. length of the foot/length of the shell) was significantly smaller in conspicuous cockles than in inconspicuous ones (Table 1, unpaired t-test, $t = 2{\cdot}77$, D.F. = 34, $P = 0{\cdot}009$). Dissection of all cockles revealed that only 1 individual did not harbour cysts of *C. australis*. In other individuals, all the cysts were found in the foot. There was no significant relationship between the parasite load and the shell length (ln + 1 transformed data, $n = 36$, $r = 0{\cdot}11$, $P = 0{\cdot}52$). However, conspicuous individuals were more heavily infected than inconspicuous ones (Table 1, Mann–Whitney test, $z = -3{\cdot}66$, $P = 0{\cdot}0003$) and overall, the relative foot length was negatively correlated with the parasite load (Fig. 1 A, ln + 1 transformed data: $n = 36$, $r = -0{\cdot}37$, $P = 0{\cdot}025$).

Field study

We did not observe crawling tracks during the sampling. Only 2 individuals in S2 and 1 in S3 did not harbour any cyst of *C. australis*. All the cysts in other individuals were found in the foot as before. Individuals in S2 were significantly smaller (Table 1, Mann–Whitney test: $z = -8{\cdot}98$, $P = 0{\cdot}0001$) and tended to be more heavily infected than those in S3 (Table 1, Mann–Whitney test: $z = -1{\cdot}44$, $P = 0{\cdot}15$). The relationship between the parasite load and the length of the shell was positive and significant for S2 (ln + 1 transformed data, $n = 48$, $r = 0{\cdot}87$, $P = 0{\cdot}0001$), while in S3 it was positive but not significant ($n = 62$, $r = 0{\cdot}22$, $P = 0{\cdot}08$).

In both S2 and S3, there was no significant difference between the mean shell length of individuals that were classified as conspicuous or inconspicuous during the sampling (Table 1, unpaired t-test, S2: $t = 0{\cdot}50$, D.F. = 46, $P = 0{\cdot}62$; S3: $t = -1{\cdot}9$, D.F. = 60, $P = 0{\cdot}07$). The parasite load of conspicuous and inconspicuous individuals was not significantly different either (Table 1, Mann–Whitney test, S2: $z = -0{\cdot}62$, $P = 0{\cdot}54$; S3: $z = -0{\cdot}05$, $P = 0{\cdot}96$). However, conspicuous individuals have, as described before, a smaller relative foot length than individuals that were inconspicuous, although this difference was significant only for S3 (Table 1, S2: t-test, $t = -0{\cdot}73$, D.F. = 46, $P = 0{\cdot}47$; S3: t-test, $t = 3{\cdot}14$, D.F. = 60, $P = 0{\cdot}0026$). For both S2 and S3, the relative foot length was negatively correlated with the parasite load (Fig. 1 B and C, ln + 1 transformed data, S2: $n = 48$, $r = -0{\cdot}64$, $P = 0{\cdot}0001$; S3: $n = 62$, $r = -0{\cdot}46$, $P = 0{\cdot}0002$).

After 3 tides (72 h), we were able to find again 93 marked cockles out of the 100 previously relocated to the experimental area (44/50 and 49/50 among individuals classified as inconspicuous and conspicuous respectively). One cockle previously classified as inconspicuous was found at the surface, while the 43 other individuals of this category were still under the sediment. Five cockles previously classified as conspicuous were found under the sediment, while the 44 other individuals of this category remained at the surface. Thus, 93·5 % of the cockles remained in their original position, indicating that this behaviour is highly repeatable in nature.

Predation test

In addition to the pied oystercatcher *Haematopus ostralegus*, we also observed the following bird species on, or near the experimental area:

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Table 1. Mean shell length, parasitic abundance and relative foot length of *Austrovenus stutchburyi* in the 3 samples

Sample	*N*	Shell size (mm) ± S.D.	Mean parasite abundance ± S.D. (and range)	Relative foot length
S1				
All data	36	41·7 ± 3·1	17·9 ± 26·9 (0–123)	0·56 ± 0·04
Conspicuous	6	39·6 ± 2·9	63·0 ± 36·7 (19–123)	0·52 ± 0·03
Inconspicuous	30	42·1 ± 3·1	8·8 ± 11·6 (0–57)	0·57 ± 0·04
S2				
All data	48	24·9 ± 7·6	201·4 ± 42·5 (0–1142)	0·45 ± 0·08
Conspicuous	31	25·4 ± 7·3	176·9 ± 284·3 (0–1142)	0·44 ± 0·08
Inconspicuous	17	24·2 ± 8·4	246·2 ± 315·3 (3–1063)	0·46 ± 0·08
S3				
All data	62	50·2 ± 3·2	17·9 ± 20·6 (0–104)	0·55 ± 0·04
Conspicuous	26	51·1 ± 3·8	20·5 ± 26·4 (0–104)	0·53 ± 0·04
Inconspicuous	36	49·6 ± 2·6	16·1 ± 15·1 (2–75)	0·56 ± 0·03

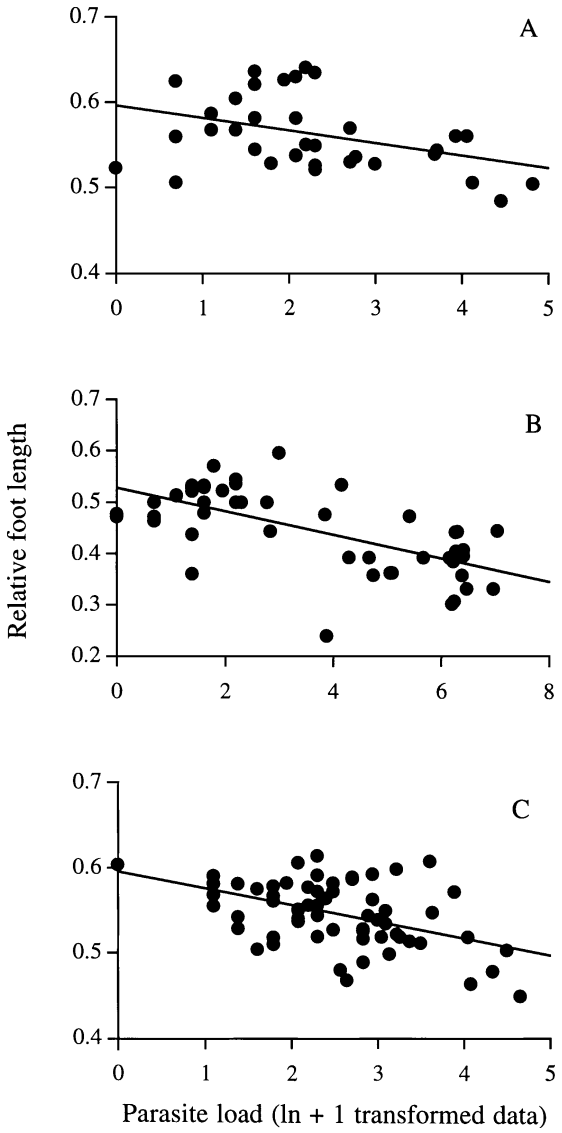


Fig. 1. Relationship between the relative length of the foot and the parasite load of *Curtuteria australis* in S1 (A), $y = -0{\cdot}014 . x + 0{\cdot}60$, S2 (B), $y = -0{\cdot}023 . x + 0{\cdot}53$ and S3 (C), $y = -0{\cdot}019 . x + 0{\cdot}60$.

spur-winged plover (*Vanellus miles*), black-backed gull (*Larus dominicanus*), red-billed gull (*Larus novaehollandiae*), white-faced heron (*Ardea novaehollandiae*), and the pied stilt (*Himantopus himantopus*).

During the 7 weeks of the test, 6 cockles at the surface and 4 under the sediment were found unglued. For 8 cockles, predation was, however, indisputable since we found fragments of the shell still attached to the string. Among these cockles, 7 were individuals previously classified as conspicuous and 1 previously classified as inconspicuous. Predation rates were significantly higher on surface (conspicuous) cockles than on buried ones (Fisher's exact test, $P = 0{\cdot}03$). Given the huge natural density of cockles at the site (several hundred per m^2), a significant result is a strong indication of the feeding preferences of birds.

DISCUSSION

Our results showed that some individuals of *A. stutchburyi* have an altered burrowing behaviour that renders them conspicuous at the surface of the sediment. A relatively small foot appeared likely to be the proximal cause of this highly repeatable behavioural alteration. When cockles are (for any reasons) at the surface, those with a stunted foot are less likely to burrow and to hide perfectly in the sediment than those with a relatively large foot. Given that (i) the trematode *C. australis* encysts exclusively in the foot of *A. stutchburyi*, (ii) the relative length of the foot is negatively correlated with the parasite load and (iii) conspicuous cockles are apparently significantly more vulnerable to predation by aquatic birds, it seems likely that *C. australis* reduces the growth of the foot in order to favour its transmission to predatory definitive hosts. The fact that in the field, cockles at the surface are not systematically more heavily parasitized than those with a normal behaviour may be due to some

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heavily parasitized individuals that have not yet been accidentally exposed at the surface by currents or brought to the surface by some other disturbance.

The possibility that the position of surface cockles results from parasite-induced photophilia has been ruled out in our laboratory test. The test showed that small-footed cockles placed under the sediment could not make their way back to the surface, where they stayed if initially placed there. The metacercariae are thus handicapping their host by reducing the growth of the foot. It is likely that heavily parasitized cockles with a relatively large foot were not exposed to cercariae when very young. The fact that we found significant effects despite the unequal exposure to parasites among cockles suggests that the metacercariae have an important impact on foot growth.

An alternative hypothesis is that cockles with a small foot could be individuals in poor condition (e.g. Mouritsen, 1997) and thus more susceptible to parasite infection compared with other individuals. The alteration of the behaviour would not be parasite induced in this case, but given the higher risk of predation of cockles with an altered behaviour, *C. australis* would obtain a higher transmission rate by infecting such individuals rather than cockles with a normal behaviour. Experimental infection of young cockles and analysis of the behaviour of the cercariae of *C. australis* in the laboratory would be necessary to address this point. The hypothesis according to which *C. australis* could be only a hitch-hiker parasite (e.g. Thomas *et al*. 1997), infecting cockles already manipulated by another parasite is unlikely here since cockles in our samples contained no other parasite. During the sampling, we found a few cockles also harbouring sporocysts of an unidentified trematode; these cockles were excluded from our study.

Several trematode species alter the behaviour of bivalves (Swennen, 1969 but see Mouritsen, 1997; Bartoli, 1974; Laukner, 1984). Although predation tests in nature have not been conducted as in the present study, it seems likely that any processes that render cockles more conspicuous at the surface of the sediment will result in an increased risk of predation by definitive hosts. In the absence of constraints, similar adaptations are expected to appear in several different lineages evolving under different selective pressures. In the previous examples (Swennen, 1969; Bartoli, 1974; Laukner, 1984), convergent evolution is apparently a likely scenario since proximal mechanisms making cockles more conspicuous at the surface are different. In the case of *C. australis*, it seems, however, likely that ability to alter behaviour was inherited since similar behavioural alterations are known in the closely related trematode *Himasthla elongata* which infects the foot of the cockle *Cardium edule* (Laukner, 1984). Although Laukner (1984) argued that the main effect of these metacercariae was mechanical, he did not analyse the relationship between the parasite load and the size of the foot. Even if manipulations in himasthline trematodes are phylogenetically inherited and not independently evolved, their adaptive value is likely to be maintained since they increase significantly the probability of successful transmission.

Our study also illustrates the importance of studying host manipulation by parasites on a larger geographical scale. As shown by Mouritsen (1997), the association between host behaviour and parasitism can vary among different localities or populations (see also Yan, Stevens & Schall (1994) for similar arguments). Our results from various samples are slightly different but overall they provide consistent support for stunting of foot growth as a parasite strategy.

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