

EFFECTIVENESS OF LADYBIRDS AS BIOLOGICAL CONTROL AGENTS: PATTERNS AND PROCESSES

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Aphidophagous species of ladybirds have generally proved ineffective biocontrol agents, whereas many coccidophagous species have proved very effective, especially *Rodolia cardinalis* (Caltagirone & Doutt, 1989). Two hypotheses have been proposed to account for this pattern: the optimum food utilization/satiation hypothesis (Mills, 1982) and the generation time ratio hypothesis (Kindlmann & Dixon, 1996). In this paper the extensive literature on ladybirds is used to test these hypotheses.

KEY-WORDS: aphids, biological control, coccids, ladybirds.

In spite of the great and long standing interest in ladybirds there have been few attempts to account for why these insects have generally been more successfully employed in the biological control of coccids than aphids (Taylor, 1935; Clausen, 1940, 1978; Hodek, 1973). Two hypotheses have been proposed: the optimum food utilisation (OFU)/satiation (Mills, 1982) and the generation time ratio (GTR) (Dixon *et al.*, 1995), hypotheses.

Optimum food utilisation: Coccidophagous species of ladybirds are reported to feed almost continuously, whereas aphidophagous species are characterised by long periods of inactivity due to satiation (Taylor, 1935; Mills, 1982). In feeding on immobile prey, coccidophagous ladybirds are thought to be more selective, concentrating on that part of their prey that is readily extracted, easily assimilated and rapidly digested. A reduction in digestion time would allow more continuous feeding, while a reduction in the proportion of each prey item eaten would increase the potential impact on the prey population. In contrast aphidophagous species tend to eat all of each item, and this non-selective feeding results in frequent satiation. This led Mills (1982) to suggest that the greater success of coccidophagous species is attributable to their more optimal use of prey.

Generation time ratio: The underlying assumption of this hypothesis is that the fittest individuals are those that are best able to harvest the limiting resource. If the ratio of generation time of the predator to that of the prey (GTR) is large, then the predator is not able to track the prey accurately and as a consequence it is not as effective, as it would be if GTR were small (Kindlmann & Dixon, 1996). Therefore, in systems where GTR is large, individual predators with shorter development times will be at a considerable selective advantage. In systems where the GTR is small there is less likely to be a strong selection

on the predators in favour of shorter developmental times. In ladybird/coccid systems the generation times of the predator and prey are comparable, whereas in ladybird/aphid systems the prey has a much shorter developmental time than the predator. In addition, in being able to mature or reach an advanced stage of development by eating one prey unit, coccidophagous species are able to track changes in the abundance of their prey more closely and as a consequence are more effective at reducing the abundance of their prey than aphidophagous species (Dixon *et al.*, 1995; Kindlmann & Dixon, 1996). In aphidophagous species there is also both a lower critical threshold of prey abundance (Dixon, 1959) and an upper critical threshold of ladybird larval abundance within a patch (Kindlmann & Dixon, 1993), which further constrains the effectiveness of aphidophagous species, by curtailing their numerical reproductive response. In this case the success of coccidophagous ladybirds is attributed to their ability to track the abundance of their prey more closely than can the aphidophagous ladybirds.

As aphidophagous and coccidophagous ladybirds belong to the same taxon, Coccinellidae, and can even belong to different genera within the same tribe, they would appear to share the same phylogenetic constraints. That is, a comparative approach can be adopted with confidence because there are likely to be fewer phylogenetic problems to confound the interpretation of the results compared with cross taxa comparisons. The rate of development of insects is affected by both food and temperature (Dixon, 1959). Although food quality is difficult to measure, temperature is easily measured. One way of removing the confounding effect of temperature is to plot developmental rate ($1/D$, where D = duration of development in days) against temperature. Differences in the slopes and elevations of the relationships for the two groups of ladybirds and their prey will then reveal the effect of differences in 'food' and/or way of life on developmental rates.

The OFU hypothesis would imply that developmental rates of coccidophagous ladybirds should be greater than those of aphidophagous species because the former process their food more efficiently than the latter. The GTR hypothesis predicts that the developmental rates of the two groups of predators should tend to approach the developmental rates of their prey and not be determined by the way they are utilised as food. In this paper the extensive literature on aphids, coccids and ladybirds is used to test the above predictions.

MATERIALS AND METHODS

The literature was surveyed for papers that cited developmental times from oviposition/larviposition to maturity for aphids and coccids, and from oviposition to adult emergence for ladybirds. The sources are given below:

Aphids: Agarwala & Bhattacharya (1994), Campbell & Hutchinson (1995), De Loach (1974), Dharma (1979), El Din (1976), Graf *et al.* (1985), Groeters (1992), Hayakawa *et al.* (1990), Hopkins (1996), Kaakeh & Dutcher (1992), Kieckhefer & Elliot (1989), Kirkland *et al.* (1981), Komazaki (1982), Leather (1980), Lorrinan (1980), Rohitha & Penman (1983), Shu-Sheng & Hughes (1987), Watson (1985), Wellings (1981).

Coccids: Ball (1980), Bodenheimer (1932), Cressman (1935), El-Minshawy & Moursi (1976), El-Minshawy *et al.* (1974), Hafez & Salama (1969), Herren *et al.* (1989), Iheagwam & Eluwa (1983), Kidd (personal communication), Lema & Herren (1985), Moutia (1944), Myers (1932), Schneider *et al.* (1987), Taylor (1935), Uichanco & Villaneuva (1932), Washburn & Frankie (1985), Yu & Luck (1988).

Aphidophagous ladybirds: Hodek (1973), Ibrahim (1955), Kapur (1942), Kawauchi (1983), Kesten (1969), Lamona & Miller (1995), McMullen (1967), Michels & Behle

(1991), Michels & Flanders (1992), Mills (1979), Naranjo *et al.* (1990), Obrycki & Tauber (1982), Okrouhla *et al.* (1983), Quilici (1981), Simpson & Burkhardt (1960), Tawfik *et al.* (1973), Whittaker (1987), Wright & Laing (1978).

Coccidophagous ladybirds: Babu & Azam (1987), Bodenheimer (1932), Booth *et al.* (1995), Chazeau (1981), Fabres & Kiyindou (1985), Heidari (1989), Izhevsky & Orlinsky (1988), Kanika-Kiamfu *et al.* (1992), Kapur (1942), Kehat (1968), Kiyindou (1989), Kiyindou & Fabres (1987), Kiyindou *et al.* (1992), Moutia (1944), Muma (1955), Nsiama She *et al.* (1984), Podoler & Herren (1983), Ponsonby (1994).

Comparison of means was carried out with one way ANOVA using Tukey HSD test to determine pairwise differences. Comparison of regression slopes was done using Tukey HSD test (Zar, 1984).

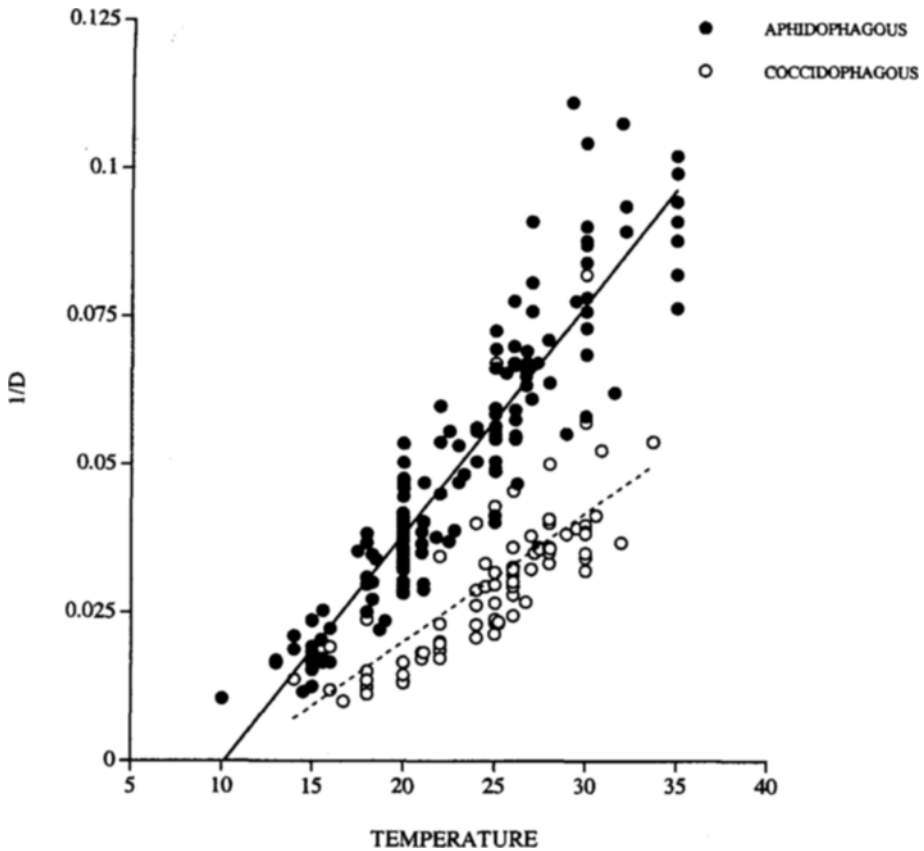


Fig. 1. The relationship between developmental rate ($1/D$) and temperature for aphidophagous and coccidophagous ladybirds (D is the number of days from oviposition to adult emergence).

RESULTS

OPTIMAL FOOD UTILISATION

The plot of the relationships between developmental rate (1/D) and temperature for 29 species of aphidophagous and 19 species of coccidophagous ladybirds, each reared at a range of temperatures, contrary to the prediction of the OFU hypothesis, indicate that aphidophagous species develop faster than coccidophagous species (fig. 1). The slopes of

TABLE 1

A - The developmental rates, at five degree intervals, over the range 15 to 30°C, and B - the slopes of the relationships between developmental rate and temperature for ladybirds and their prey. Values in the same row followed by different letters in parenthesis differ significantly ($P < 0.05$)

A Developmental rates (1/D)

Temperature °C	Ladybirds		Prey	
	Aphidophagous	Coccidophagous	Aphids	Coccids
15-20	0.0343 (b)	0.0182 (c)	0.0885 (a)	0.0117 (c)
20-25	0.0491 (b)	0.0274 (c)	0.1356 (a)	0.0192 (c)
25-30	0.0673 (b)	0.0366 (c)	0.1663 (a)	0.0252 (d)

B Slope of the relationships 1/D against temperature

0.0039 (b)	0.0022 (c)	0.0072 (a)	0.0014 (d)
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TABLE 2

The developmental time in day degrees (D°) above 0°C, and the average temperature at which the species in each group were reared for ladybirds and their prey. Values in the same column followed by different letters in parenthesis differ significantly ($P < 0.05$)

		Developmental time (D° above 0°C)	Average temperature used for rearing
Ladybirds	Aphidophagous	536.34 ± 34.8 (c)	22.82 (b)
	Coccidophagous	906.8 ± 46.8 (b)	24.87 (a)
Prey	Aphids	219.32 ± 33.29 (d)	18.4 (c)
	Coccids	1,588.1 ± 45.9 (a)	23.92 (a,b)

these two relationships differ significantly. In addition, over the range of temperatures at which most of the observations were made, 15-30°C, the aphidophagous species developed significantly faster than the coccidophagous species in each five degree interval (table 1). This difference is also reflected in their developmental times in day degrees. Lower thermal thresholds have been calculated for very few ladybirds, however, if a common threshold of 0°C is assumed then the developmental times is on average significantly 1.7 times longer in coccidophagous species (table 2). In view of the clear difference in the developmental times of most aphidophagous and coccidophagous ladybirds it would be interesting to know more about *Coleophora quadrivittata*, which is the only coccidophagous species that does better than the average aphidophagous species.

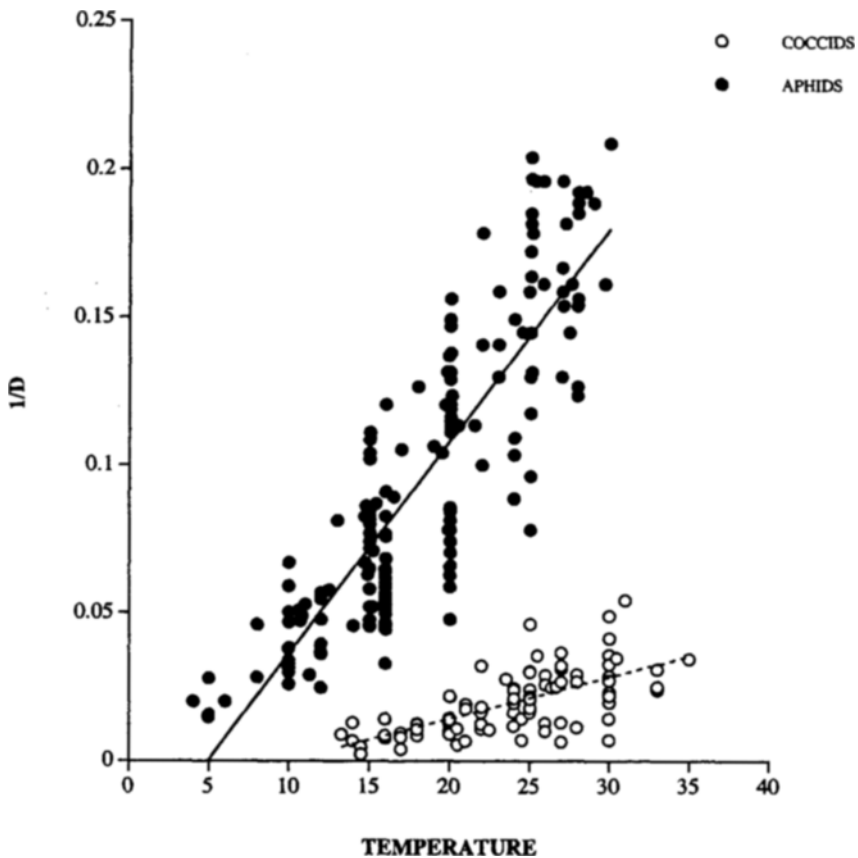


Fig. 2. The relationship between developmental rate ($1/D$) and temperature for aphids and coccids (D is the number of days from birth or oviposition to the onset of reproduction).

GENERATION TIME RATIO

The plot of the relationships between developmental rate and temperature for aphids and coccids clearly reveals that aphids generally develop much faster than coccids (fig. 2).

Although coccids were generally reared at higher temperatures than aphids (table 2) the differences in developmental rate at 5° intervals over the range 15 to 30°C are significant and very large (table 1). When development time is measured in day degrees above 0°C aphids develop some 7 times faster than coccids. Thus the prey are very different in the time they take to reach maturity.

Although aphidophagous ladybirds develop much faster than coccidophagous species the slope of the relationship for aphidophagous species differs significantly from that for aphids and the developmental rates are significantly less measured over 5° intervals from 15 to 30°C (fig. 3; table 1). In marked contrast, although the relationships for coccidophagous ladybirds and coccids have significantly different slopes, their developmental rates only differ significantly at the higher temperatures when the predators develop faster than the prey (fig. 4; table 1). That is, relative to their prey coccidophagous ladybirds develop as fast at low temperatures and faster at high temperatures. This observation conforms with the GTR hypothesis' prediction that the developmental rates of these two groups of closely related predators should reflect that of their prey, with the aphidophagous species developing faster than the coccidophagous species.

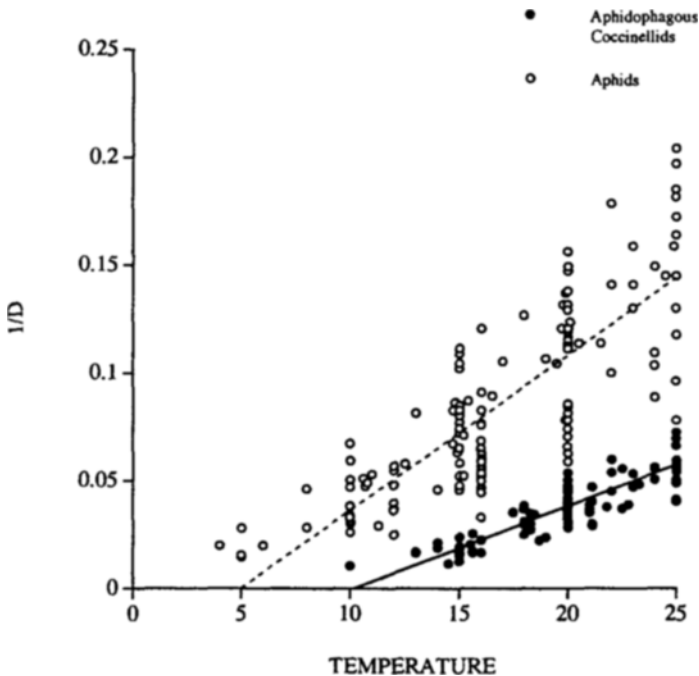


Fig. 3. The relationship between developmental rate ($1/D$) and temperature for aphids and aphidophagous ladybirds.

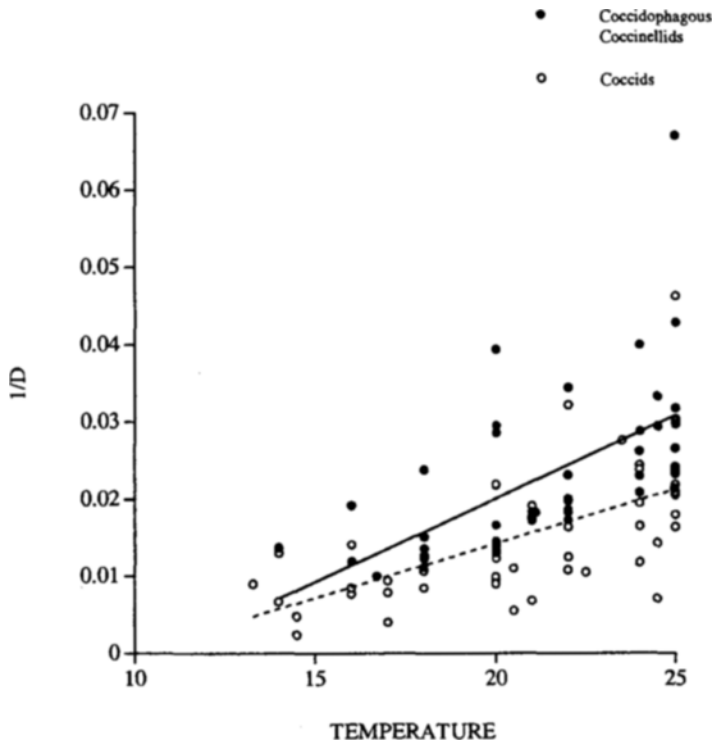


Fig. 4. The relationship between developmental rate ($1/D$) and temperature for coccids and coccidophagous ladybirds.

DISCUSSION

This comparative study has revealed very clear patterns. Aphids develop very much faster than coccids, which is mainly a consequence of aphids having evolved telescoping of generations (Kindlmann & Dixon, 1989). More surprisingly the ladybird predators of aphids and coccids also differ in their developmental rates, with those feeding on aphids developing faster than those feeding on coccids. That is, their developmental rates reflect that of their prey.

It is possible to select for faster development in ladybirds (Rodriguez-Saonia & Miller, 1995). Although their study did not reveal a cost in terms of reduced performance in another life history trait, theory predicts such a trade-off. The fittest individuals are likely to be those that most effectively harvest their prey (cf. Kindlmann & Dixon, 1996). Thus the upper points in the relationship for aphidophagous ladybirds in figs. 1 and 3 are likely to be close to the fastest achievable by ladybirds. As the developmental rates of coccids are considerably slower than those for aphids the developmental rates of coccidophagous ladybirds have not been subjected to the same intense selection. On average their development rates are faster than those of their prey, which makes it possible for them to be

effective biological control agents. Expect for the two values for *Coelophora quadrivittata* the upper bound to the values for coccidophagous ladybirds in fig. 4, like that for aphidophagous ladybirds in fig. 3, appears to be very clearly demarcated. That is, the coccidophagous ladybirds could develop faster. What the cost(s) to developing faster is in these ladybirds remains to be discovered.

The process underlying the marked difference in the developmental rates of aphidophagous and coccidophagous ladybirds is unknown. Life history theory indicates a possible mechanism. Adults of aphidophagous ladybirds are on average larger than those of coccidophagous species (Dixon & Hemptinne, unpublished). Assuming both groups of ladybirds have similar growth rates, indicated by the slope of the relationships in fig. 5A, then aphidophagous ladybirds might lay considerably larger eggs than coccidophagous species ($E_A > E_C$), because in the former there are advantages in having a shorter developmental time and being large enough at birth to pursue and subdue their prey, neither of which are as important for coccidophagous ladybirds. The consequence of this relative difference in egg size is that even with a greater developmental time coccidophagous ladybirds ($D_C > D_A$) could still be smaller as adults ($W_A > W_C$; fig. 5A). Alternatively, aphidophagous ladybirds lay smaller or similar sized eggs ($E_A = E_C$) but the growth rate that can be sustained by eating coccids is inferior to that when eating aphids. The consequence of this is that even with a longer development time ($D_C > D_A$) coccidophagous ladybirds could still be smaller as adults ($W_A > W_C$; Fig. 5B). Interestingly, this depends on a difference in food quality the reverse of that assumed by the OFU hypothesis. As with other life history traits selection will favour those individuals that are better able to handle and utilize their prey, be it aphid or coccid. This is likely to result in the quality of the prey for these specialist predators being very similar.

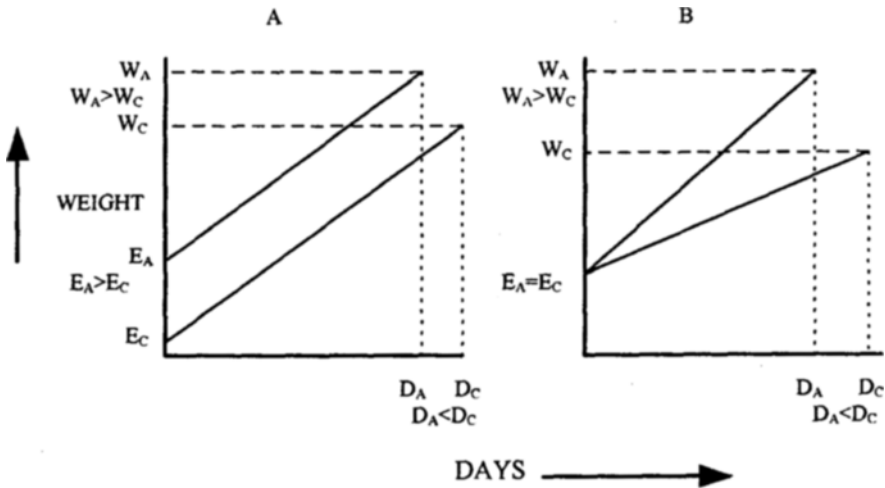


Fig. 5. The relationships between adult weights (W_A , W_C) and developmental times for: ladybirds reared at one temperature on food of the same quality but starting with eggs of different weights (E_A , E_C), where $E_A > E_C$ and D_A and D_C are the developmental times (A); and at one temperature, starting with eggs of the same or different weights ($E_A < E_C$) and the ladybirds experiencing different qualities of food (B) (E_A , D_A , W_A -aphidophagous ladybird; E_C , D_C , W_C -coccidophagous ladybird; the relative growth rate is indicated by the slope of the line).

Although there is very little understanding of the process underlying the marked difference in the developmental rates of aphidophagous and coccidophagous ladybirds it is unlikely to be a consequence of a difference in food quality. However, whatever the process, theory (Kindlmann & Dixon, 1996) predicts that coccidophagous ladybirds in having a developmental rate that is faster or similar to that of their prey are able to reduce the abundance of their prey to greater extent than the aphidophagous ladybirds, all of which have considerably slower developmental rates than their prey. That is, coccidophagous ladybirds are more likely to be effective biocontrol agents than aphidophagous ladybirds.

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RÉSUMÉ

Efficacité des coccinelles comme agents de lutte biologique

Chez les coccinelles, les espèces aphidiphages se sont montrées généralement peu efficaces comme agents de lutte biologique, à l'inverse de nombreuses espèces coccidiphages qui se sont révélées très efficaces, telle *Rodolia cardinalis* (Caltagirone & Doutt, 1989). Deux hypothèses ont été proposées pour expliquer ce phénomène : l'hypothèse de l'utilisation optimale de la proie/ satiété (Mills, 1982) et l'hypothèse du rapport des durées de développement des générations (Kindlmann & Dixon, 1996). Dans cette étude, la vaste littérature existant sur les coccinelles est utilisée pour tester ces hypothèses.

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