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INSTAR-SPECIFIC DEFENSE OF *COLEOMEGILLA MACULATA LENGI* (*COL.: COCCINELLIDAE*): INFLUENCE ON ATTACK SUCCESS OF THE INTRAGUILD PREDATOR *CHRYSOPERLA RUFILABRIS* (*NEUR.: CHRYSOPIDAE*)

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We conducted a laboratory study of the behavioural interactions between larval stages of the lady beetle *Coleomegilla maculata lengi* Timberlake and an intraguild predator, the lacewing *Chrysoperla rufilabris* Burmeister. Ladybird susceptibility to predation by third instar *C. rufilabris* is age-specific and influenced by larval defensive strategies. First and second instars of *C. maculata* were captured more consistently by chrysopid larvae than third and fourth instars. Young coccinellids generally exhibit escape reactions (dropping, fleeing, retreating) but, do not survive after being caught by lacewings. In addition to escape reactions, older larvae may actively defend themselves by wriggling or biting, even after being pierced. The proportion of physical interactions that resulted in coccinellid death was significantly lower for older instars (< 2%) than for first (35%) and second (19%) instars. Capture efficiency by *C. rufilabris* was related to the coccinellid-chrysopid size ratio. Dropping off the leaves, the most common defensive behaviour displayed by coccinellid larvae, contributed to reduce overall mortality of first instars to a level similar to the one observed for older stages. However, lacewings were able to prevent coccinellid dropping by impaling and holding their prey in the air, or by falling with the ladybirds to the ground where they continued their attack.

KEY-WORDS: intraguild predation, aphid predator, escape behaviour, defensive strategy.

With the exception of rare superpredators, predatory organisms are also vulnerable to predation (Polis *et al.*, 1989; Laurensen, 1994). When a predator kills and consumes another predator belonging to the same guild (exploiting the same prey), the interaction is termed intraguild predation (Polis *et al.*, 1989; Polis & Holt, 1992). Aphidophagous species, because of their diversity and abundance in the vicinity of aphid colonies, are likely to be involved in intraguild predation (Rosenheim *et al.*, 1993; 1995; Lucas *et al.*, 1997). Predator mobility, size and feeding specificity are the main ecological characteristics which determine the outcome of intraguild confrontations in aphidophagous insects (Lucas *et al.*, 1997).

Arthropods have evolved an array of morphological, chemical and behavioural defensive mechanisms to avoid predation and parasitism (Edmunds, 1974; Endler, 1986, 1991; Sih, 1987). The type of defensive strategy used varies during the course of development of an organism. The maximum size of prey attacked by a predator generally increases with the size (and hence the age) of the predator (Sabelis, 1992). Concurrently, prey mobility and vigor increase with size, which enhances the efficiency of defensive strategies. For example, the nature, frequency and efficiency of defensive behaviours (walking, kicking, dropping) of the pea aphid, *Acyrtosiphum pisum* Harris, toward the predatory bug, *Anthocoris nemorum* L., depend upon the relative sizes of the predator and prey (Evans, 1976), aphid kicking behaviour being more efficient when the predator-prey size ratio is low (see also Dixon, 1958). Similarly, reactions of the basswood aphid, *Eucallipterus tiliae* L., to an attack by the lady beetle, *Adalia bipunctata* L., vary according to the size of the protagonists (Wratten, 1976). Kicking behaviour was exhibited only against first and second instar coccinellids, running was more frequently displayed when the predator-prey size ratio was low and, conversely, jumping was used when the ratio was high.

We studied the behavioural defensive strategies of the different larval stages of the spotted lady beetle, *Coleomegilla maculata lengi* Timberlake (Coleoptera: Cocccinellidae), against a sympatric intraguild predator, the lacewing, *Chrysoperla rufilabris* Burmeister (Neuroptera: Chrysopidae). As shown by Lucas *et al.* (1997), eggs, larvae, pupae and adults of the spotted lady beetle are vulnerable to attacks by lacewing larvae. Levels of intraguild predation between lacewing third instar larvae and spotted lady beetle larvae exceeded 90%.

The objective of the present study was to examine the instar-specific defensive capacity of *C. maculata*. We predicted that the 1) vulnerability of coccinellid larvae decreases with age, 2) defensive behaviour of the coccinellid larvae changes with age as their vigor and escape capacity increase, fighting behaviour being restricted to older instars. These predictions were tested in the laboratory by observing behavioural interactions between *C. maculata* larvae (I, II, III, IV instars) and third instar of the lacewing *C. rufilabris.*

MATERIAL AND METHODS

Chrysoperla rufilabris and *Coleomegilla maculata* originated from commercial rearings (Biocontrôle inc., Québec, Canada) and were reared under laboratory conditions at 23°C (16L: 8D) and fed potato aphids, *Macrosiphum euphorbiae* Thomas. Predators were allowed to feed for 24 h following eclosion (Ist instar) or moulting (II, III, IV instars), after which they were starved for 24 h prior to the test in order to increase their motivation to search for prey. No extraguild prey (aphids) were used during the experiments in order to maximize *C. maculata* - *C. rufilabris* interactions. All experiments were carried out at 24°C.

The first experiment was aimed at comparing, on a plant, the survival and defensive strategies exhibited by I, II, III and IV larval instars of the spotted lady beetle when in the presence of a lacewing third instar larva. The experimental arena consisted of a 7 to 10 cm high potato plant (cv. Norland), trimmed in such a way that only one horizontal leaf remained (ca 6 × 5 cm). Tests started by introducing a coccinellid larva in the center of the upper surface of the leaf and a chrysopid larva on the stem, with its head directed toward the leaf. Tests lasted a maximum of 30 minutes, but could be terminated earlier with 1) the dropping of the coccinellid to the ground following contact, an attack or a very close encounter (< 2 mm) with the chrysopid, 2) the escape of the coccinellid toward the base of the stem following conditions similar to dropping, or 3) the death of the coccinellid after an attack by the chrysopid. A test was considered valid when the chrysopid came into contact with the coccinellid (anterior part), or when the coccinellid reacted to a light brush by the chrysopid.

Following every approach or attack by chrysopid larvae, we characterized the behaviour displayed by coccinellid larvae. Successful defensive behaviours were classified as:

- Retreating: the coccinellid moved back, over a short distance (< 2 cm), without turning around;
- Fleeing: the coccinellid turned around and moved over a long distance (> 2 cm);
- Dropping: the coccinellid dropped to the ground;
- Biting: the coccinellid bit or attempted to bite the chrysopid with its mandibles;
- Wriggling: the coccinellid wriggled either to prevent the chrysopid from strengthening its hold or to free itself.

Coccinellid instar-specific vulnerability was evaluated by comparing mortality and the proportion of lethal contacts, that is, the number of contacts having resulted in the death of the coccinellid over the total number of contacts during the test. These parameters were compared using goodness of fit tests. If there were significant differences, then the means were compared by using the G-test additivity rule for degrees of freedom (Scherrer, 1984). Fifteen replicates were done for each treatment and predators were used only once.

A second experiment was aimed at comparing coccinellid instar-specific survival depending on whether interactions with chrysopid larvae occurred on the lower or upper leaf surface. The coccinellid could drop only when on the lower surface. A Petri dish (7 cm in diameter), the sides of which were coated with fluon, served both as the "upper surface" (Petri right side up) and as the "lower surface" (Petri upside down).

The coccinellid was first introduced in the Petri dish, followed by the chrysopid at the opposite section. Tests lasted 15 minutes and ended with the death of one of the predators or the dropping of the coccinellid. Conditions for determining the validity of the test were the same as for the preceding experiment.

For each larval stage, the mortality on the lower surface was compared to that on the upper surface (G-test). Mortality was further compared between larval stages (goodness of fit). The proportion of coccinellids having dropped from the lower surface was compared, according to coccinellid instar, using a G-test. Fifteen to seventeen replicates per surface were carried out for each coccinellid instar.

RESULTS

Coccinellid mortality on plants differs significantly according to the larval stage involved ($G_3 = 10.9$, $P < 0.02$). Mortality of first and second instars (47%) was significantly higher than that of third and fourth instars (< 15%) (fig. 1A). Similarly, the percentage of fatal contacts decreased significantly with larval age ($G_3 = 35.5$, $P < 0.0001$) (fig. 1B). No lacewing was killed during encounters with coccinellids. The outcome of confrontations differed markedly according to the larval stage involved. In all cases, young instars (I and II) were expelled from the plant, either by being killed or following escape (dropping and fleeing), whereas 28% and 56% of third and fourth instar larvae, respectively, remained on the leaf after 30 minutes (fig. 2).

In Petri dishes, larval mortality was lower on the bottom surface than on the top surface. Mortality decreased significantly by 73% for first instars ($G_1 = 18.7$, $P < 0.0001$) and by 47% for fourth instars ($G_1 = 9.95$, $P < 0.01$). A similar tendency was observed for second and third instars, although the decrease was not significant. As with the preceding experiment, mortality of coccinellids introduced on the upper surface decreased with larval age ($G_3 = 9.97$, $P < 0.04$) (fig. 3). However, the vulnerability of all stages was similar on the lower surface ($G_3 = 7.81$, $P > 0.08$).

The nature and frequency of successful defensive behaviours differ according to coccinellid instar (fig. 4). Differences are observed essentially between young (I and II) and old

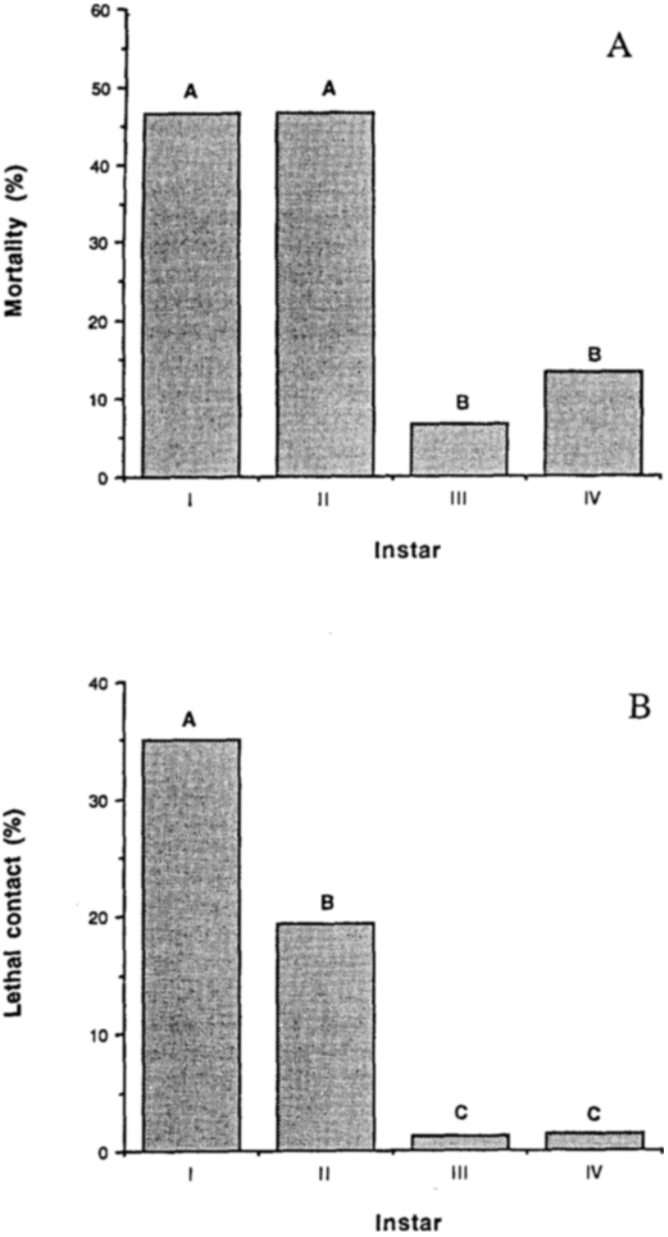

Fig. 1 Vulnerability of *Coleomegilla maculata* larvae in the presence of third instar *Chrysoperla rufilabris*. (A) Mortality (%), (B) Lethal contact (%). Percentages followed by different letters are significantly different (G-Test, $P < 0.05$).

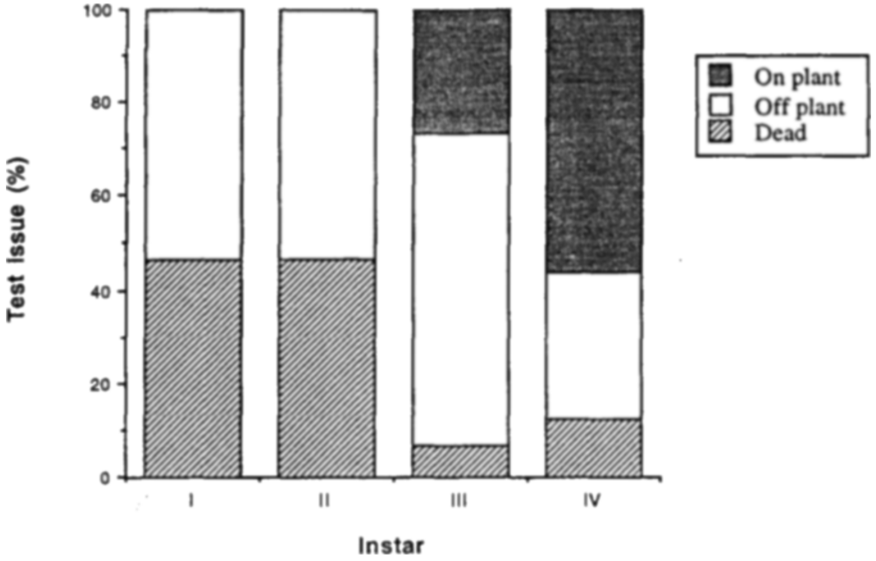

Fig. 2. Percentage of *Coleomegilla maculata* larvae that were found on the plant, off the plant or dead following an interaction with third instar *Chrysoperla rufilabris*.

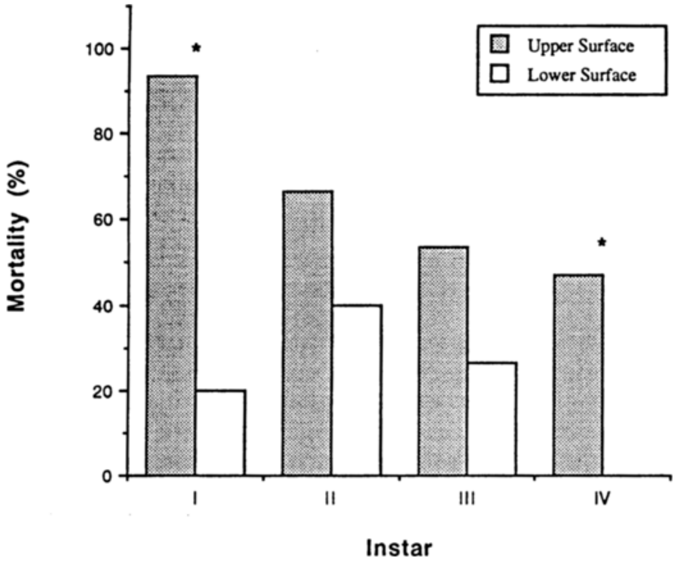

Fig. 3. Mortality (%) of *Coleomegilla maculata* larvae in the presence of third instar *Chrysoperla rufilabris* on the upper and lower surface of a Petri dish. Asterisks indicate significant differences between groups (G-Test, $P < 0.05$).

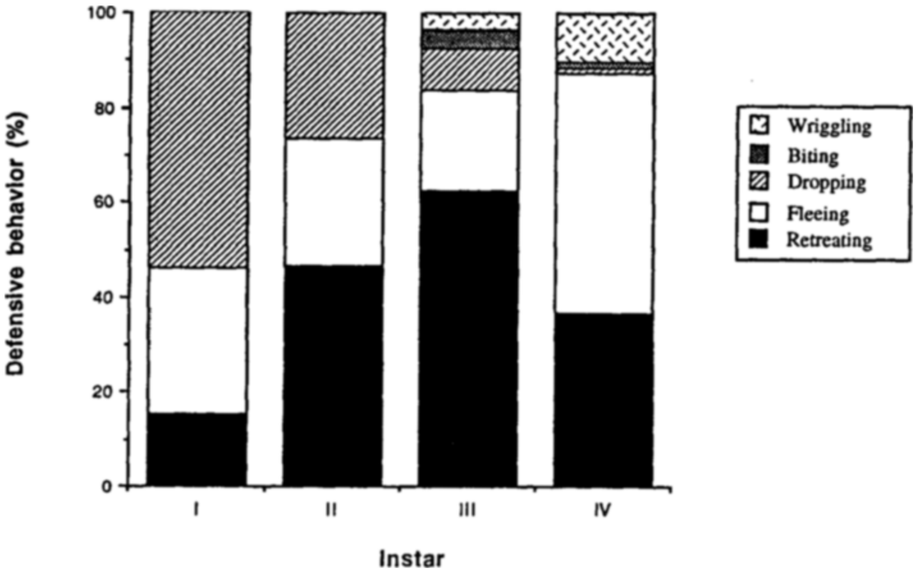

Fig. 4. Percentage of successful defensive behaviours displayed by *Coleomegilla maculata* larvae in the presence of third instar *Chrysoperla rufilabris*.

(III and IV) instars. Escape reactions (retreating, fleeing & dropping) accounted for all of the defensive behaviours used successfully by first and second instars. They also represent the great majority of defenses employed by older larvae. Third and fourth instars exhibited two different types of defense: biting and wriggling, which represent 7.5% and 11.0% respectively of the defensive behaviour they used.

In Petri dishes, during the tests carried out on the lower surface, there was no significant difference between the coccinellid instars in the use of dropping as a means of escaping the lacewing. Proportions ranged from 53% to 93% ($G_3 = 0.91$, $P > 0.80$).

DISCUSSION

Our experiments show significant variation both in vulnerability and defensive behaviour of *C. maculata* larval stages. Consistent with our prediction, vulnerability of lady beetle larvae decreased with age. Such a pattern may result from morphological and/or behavioural differences between stages.

In arthropods, size is a key factor in predator-prey interactions and, if we exclude ambush and trap-building species as well as those that use venom or hunt in groups, the great majority of predators attack lower-sized prey, against which they are the most efficient (Sabelis, 1992). During larval development, lady beetles, like most aphidophagous insects (Syrphidae, Cecidomyiidae, Chrysopidae, Hemerobiidae), undergo a considerable increase in size, which is accompanied by an increase in speed mouvement and vigour. In our tests, smaller (younger) lady beetle larvae were much more vulnerable than larger (older) larvae. Canard & Duelli (1984) have shown that predation efficiency of a lacewing larva (proportion of successful attacks per encounter) is nearly 100% when the lacewing/prey size ratio is high, whereas it may fall to less than 10% with larger prey or with prey that actively defend themselves. Similarly, during heterospecific confrontations between coccinellids, Agarwala & Dixon (1992) have also observed that the youngest larvae were the most vulnerable.

As shown by Lucas *et al.* (submitted), when opponents were of similar size (Coccinellid III × Chrysopid III), or when the coccinellid larva was bigger than the chrysopid larva (Coccinellid IV × Chrysopid III), coccinellids were most often killed by chrysopids. Sengonca and Frings (1985) also noted the superiority of *Chrysoperla carnea* Stephens larvae over *Coccinella septempunctata* L. larvae with similar vigour. A possible explanation lies in the conformation of the mouthparts of the two species. Lacewings possess very elongated hook-like mouth parts, which allow them to capture prey at a certain distance from the insect's body (Gepp, 1984). Furthermore, once integuments are pierced, prey have difficulty freeing themselves from lacewings. On the other hand, coccinellids possess crushing-type mouthparts (Iablokoff-Khnzorian, 1982) which do not permit attacks from a distance. Thus, large body size does not appear to be a dissuasive defense for spotted lady beetles against lacewings, as observed in other predator-predator interactions (Pearson, 1988).

Besides morphological characteristics, defensive behaviours of lady beetle larvae change with age. In our experimental set-ups, lady beetles could defend either during the attack phase *per se,* or during the subjugation phase. Young larvae (I and II instars) cannot actively defend themselves successfully during the subjugation phase, and must therefore escape prior to actual contact with the aggressor. On the other hand, older larvae (III and IV instars) possess two types of relatively efficient behavioural defenses: escape-type behaviours which occur during an attack and aggressive behaviours which occur during subjugation and provide older larvae with an additional opportunity to escape from predation. The most efficient defensive strategies are generally those involving several mechanisms (Gross, 1993). The absence of efficient aggressive defenses in young larvae is also observed in insects attacked by parasitoids, for which aggressive behaviours are more efficient in older larvae than young larvae (Gross, 1993). Oviposition success of *Aphelinus asychis* Walker (Aphelinidae) on the pea aphid, *A. pisum,* is lower when attacking large than small aphid nymphs (Gerling *et al.,* 1990). Escape behaviours were the principal defensive reactions of all lady beetle larval stages. This is a very common pattern in arthropods, be they herbivores (Norman, 1995) or predators (Pearson, 1988; New, 1991; Lovei & Sunderland, 1996).

Dropping represents a major and efficient component of the spotted lady beetle defensive strategy, particularly for young larvae. It allows coccinellid larvae to instantly leave the searching area of other intraguild predators. Contrary to retreating, fleeing or fighting behaviours, which depend upon the motor capacities and the vigour of the individual, dropping is independent of the age/size of the attacked larva. However, dropping to the ground does not have the same consequences for a first instar larva than for a fourth instar larva. Survival of the larva after dropping is dependent upon the risks of predation by ground predators (see Winder, 1990; Winder *et al.,* 1994), dessication (Roitberg & Myers, 1979) and on the capacity of the larva to find another feeding site. Older coccinellid larvae are better equipped to escape from predators, to survive abiotic stresses and, furthermore, they have greater autonomy. Risks associated with dropping are therefore lower for older larvae. In some instances, the lacewing circumvented the dropping behaviour of lady beetles either by falling with its prey without releasing it, or by holding the lady beetle in the air with its buccal hooks until the prey died. Five drops out of 72 (6.9%), involving at least each larval instar once, were thus prevented.

For third and fourth coccinellid instars, 7.5 and 11.0% respectively of the successful defensive strategies involved aggressive behaviour. In predatory arthropods, the use of fighting as a defense during interspecific interactions is common, for example in earwigs (Barnard, 1983), tiger beetles (Pearson, 1988), ground beetles (Lovei & Sunderland, 1996), Nabids (Lattin, 1989) and predatory ants (Hölidobler & Wilson, 1990). An aggressive defense requires the appropriate weapons (Sih, 1987), and predators, because of their mode of survival, possess natural weapons intended to kill prey or to be used as a means of defense.

Fighting-type defenses, nevertheless, represent ultimate defenses (Alcock, 1984) and, for the victim, it is preferable to interrupt the predation sequence in its initial phases since risks of mortality or injuries, as well as the amount of energy required, increase with fighting (Endler, 1991). In our study, the use of second-line defenses (fighting) represents less than 11% of all defenses used successfully.

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RÉSUMÉ

Stratégies défensives des différents stades larvaires de *Coleomegilla maculata lengi* (Col.: Coccinellidae) : influence sur le succès d'attaque du prédateur intraguilde *Chrysoperla rufilabris* (Neur.: Chrysopidae)

Le comportement des différents stades larvaires de la coccinelle *Coleomegilla maculata lengi* Timberlake a été étudié en laboratoire lors de confrontations avec un prédateur intraguilde soit le chrysope *Chrysoperla rufilabris* Burmeister. La susceptibilité des larves de coccinelle décroit avec l'âge et dépend des stratégies défensives utilisées par la larve. Les larves de stades I et II étaient capturées significativement plus souvent par le chrysope que les larves de stades III et IV. A l'approche d'un chrysope, les jeunes stades démontraient généralement une réaction d'évitement (chute, fuite ou retraite) et ne survivaient pas après avoir été capturés. Les larves plus âgées utilisent, outre les comportements d'évitement, une stratégie défensive plus aggressive en se contorsionnant ou en mordant le chrysope. La proportion de contacts causant la mort de la coccinelle s'avérait moindre pour les stades âgés (< 2 %), que pour les premiers (35 %) et seconds stades larvaires (19 %). L'efficacité de capture de *C. rufilabris* était reliée au ratio de taille coccinelle/chrysope. La chute, lorsqu'elle était possible, constituait la principale défense employée par tous les stades. Elle permettait au premier stade larvaire de diminuer sa mortalité à un niveau comparable aux stades plus avancés. Néanmoins, à plusieurs occasions, le chrysope est parvenu à contourner cette défense en maintenant la coccinelle dans les airs, ou en se laissant tomber avec elle, pour poursuivre l'attaque au sol.

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