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SHORT COMMUNICATION

Host pollination mode and mutualist pollinator presence: net effect of internally ovipositing parasite in the fig–wasp mutualism

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Abstract The *Ficus*–their specific pollinating fig wasps (Chalcidoidea, Agaonidae) interaction presents a striking example of mutualism. Figs also shelter numerous non-pollinating fig wasps (NPFW) that exploit the fig–pollinator mutualism. Only a few NPFW species can enter figs to oviposit, they do not belong to the pollinating lineage Agaonidae. The internally ovipositing non-agaonid fig wasps can efficiently pollinate the *Ficus* species that were passively pollinated. However, there is no study to focus on the net effect of these internally ovipositing non-agaonid wasps in actively pollinated *Ficus* species. By collecting the data of fig wasp community and conducting controlled experiments, our results showed that internally ovipositing *Diaziella bizarrea* cannot effectively pollinate *Ficus glaberrima*, an actively pollinated monoecious fig tree. Furthermore, *D. bizarrea* failed to reproduce if they were introduced into figs without *Eupristina* sp., the regular pollinator, as all the figs aborted. Furthermore, although *D. bizarrea* had no effect on seed production in shared figs, it significantly reduced the number of *Eupristina* sp. progeny emerging from them. Thus, our experimental evidence shows that reproduction in *Diaziella* depends on the presence of agaonid pollinators, and whether internally ovipositing parasites can act as pollinators depends on the host fig's pollination mode (active or passive). Overall, this study and others suggest a relatively limited mutualistic role for internally ovipositing fig wasps from non-pollinator (non-Agaonidae) lineages.

Keywords Agaonidae · *Diaziella* · *Ficus glaberrima* · Fig wasp · Mutualism · Pollination

Introduction

The association between pollinating fig wasps (Agaonidae) and their host fig trees (*Ficus*, Moraceae) represents a remarkable example of mutualism and co-evolution, each needing the other for reproduction (Galil 1977; Janzen 1979; Weiblen 2002; Herre et al. 2009). Figs, the inflorescences of *Ficus* species, have a unique structure, forming a hollow ball lined with hundreds of tiny flowers. For pollination to occur, pollen must be transported through the narrow entrance gate (ostiole) into a fig. *Ficus* trees depend on agaonid wasps for pollination and, therefore, viable seed production, whilst agaonid wasps depend on fig inflorescences to provide food for their larvae. Each fig species is typically pollinated by a single species of agaonid, though the number of exceptions to this one to one relationship is increasing (Compton 1990; Compton and Ware 1992; Michaloud et al. 1996; Kerdelhué et al.

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1999). Recently, genetic work based on extensive sampling of fig wasp associated with several Neotropical host fig taxa has shown the presence of previously undetected cryptic pollinating fig wasp species (Molbo et al. 2003). Many fig species have turned out to be pollinated by more than one fig wasp species (Haine et al. 2006; Machado et al. 2005; Su et al. 2008).

Some agaonids are active pollinators; when female flowers are receptive, pollen-loaded females of the agaonids are attracted to and enter the fig. Once inside, they deposit eggs within the ovules of some of the flowers (inducing the formation of galls which support the development of their progeny) and they also discharge some pollen with their forelegs (Frank 1984). Passive pollinators show no such behaviour (Galil and Neeman 1977; Kjellberg et al. 2001; Jousselin et al. 2004). When actively pollinating fig wasp progeny reach adulthood, they go to the anthers and pick up the pollen with their forelegs, deposit it on the ventral part of the thorax and shovel it into the mesothoracic pollen pockets using their fore coxae. When they enter a receptive fig, they actively remove pollen from their pollen pockets and apply it to the stigmatic surfaces of the flowers. Passive pollinators lack these behaviours. Active pollination is much more efficient, allowing their host figs to produce far fewer male flowers as less pollen is required. The mode of pollination occurring in a species of *Ficus* can be consistently predicted from the anther-to-ovule ratio (Kjellberg et al. 2001). On a representative number of fig species, these authors showed that an anther-to-ovule ratio less than 0.16 indicates active pollination, whilst a ratio over 0.20 is characteristic of passively pollinated species.

In addition to pollinating fig wasp species, figs host a suite of parasites of the mutualism (West et al. 1996) belonging to other chalcidoid families (Rasplus et al. 1998). As with the agaonids, these fig wasps develop in fig flowers, but do not usually pollinate their hosts, hence they are commonly called non-pollinating fig wasps (NPFW). Most non-agaonid wasps oviposit through the fig wall from outside the fig. Some NPFW reproduce by inducing gall formation in the fig in which their progeny develop (gallers), others appear to compete directly with the pollinator progeny for ovules for the development of their progeny (inquilines) and others appear to directly consume pollinator progeny (parasitoids) (Compton and van Noort 1992; West and Herre 1994). In essentially all careful studies, the non-pollinator species net effect is primarily to reduce the pollinator production (male function) of the figs (West and Herre 1994; West et al. 1996; Kerdelhue and Rasplus 1996; Harrison and Yamamura 2003). Alternatively, they either drain resources that could support either pollinator progeny or seeds or they parasitise other non-pollinator wasps of the fig–agaonid mutualism (Compton and van Noort 1992; West and Herre 1994; West et al. 1996; Herre et al. 2009).

A small number of non-agaonid fig wasps are exceptional in that, like agaonids, they routinely provide pollination service to their hosts (Jousselin et al. 2001; Zhang et al. 2008). These non-pollinating fig wasp species do not belong to the agaonid lineage. They have foundresses that enter the figs and oviposit in the female flowers, just as agaonid wasps do. Similar morphological adaptations have arisen between these internally ovipositing non-agaonid wasps and agaonid wasps, such as a flattened head, smooth bodies, spurs on the legs and often mandibular modifications (van Noort and Compton 1996).

Non-agaonids that enter the figs have the potential to act as pollinators and Jousselin et al. (2001) reported that six species of *Ficus* were pollinated not only by agaonids (*Waterstoniella* spp.) but also by non-agaonids belonging to the genera *Diaziella* (Pteromalidae, Sycoecinae) and *Lipothymus* (Pteromalidae, Otitesellinae), thereby suggesting that *Ficus* have the potential to form mutualisms with other groups of fig wasps. Biological data on the genera *Diaziella* and *Lipothymus* wasps is limited. Both belong to groups of fig wasps that are assumed to generally develop inside ovules galled by ovipositing females. Basing on their conclusions and inferences, Zhang et al. (2008) conducted experiments and the result has shown that a *Ficus* species with a *Eupristina* agaonid is also pollinated efficiently by *Diaziella yangi* (van Noort et al. 2006) and a *Lipothymus* sp. However, contrary to inferences from the observations from Jousselin et al. (2001), the experiments from Zhang et al. (2008) showed that both the *Diaziella* and *Lipothymus* species could not develop in figs that had not been entered by the pollinating agaonid in the passively pollinated figs. Furthermore, both species reduced the numbers of pollinator progeny (but had no effect on seed production).

Those *Diaziella* and *Lipothymus* species that are known to be able to act as pollinators develop in passively pollinated fig species that produce abundant pollen. (Jousselin et al. 2001; Zhang et al. 2008). Jousselin et al. (2001) assumed that *Diaziella* species cannot be effective pollinators in actively pollinated fig species.

In this study, we conducted experimental introductions in order to study the relationships between the actively pollinated host fig (*Ficus glaberrima*), its regular agaonid pollinator, *Eupristina* sp., and the internally ovipositing, *Diaziella bizarrea* (van Noort et al. 2006), to ask: (1) Is *D. bizarrea* as reliable a pollinator of *F. glaberrima* as the plant's agaonid wasp (an undescribed species of *Eupristina*)? (2) Can *D. bizarrea* reproduce independently of the agaonid? (3) What is the effect of *D. bizarrea* on the agaonid and the *Ficus*–agaonid mutualism? Ultimately, by comparisons with previous experimental and correlative studies, we attempt to address the question of why there are no known fig tree species which are totally independent of agaonid pollinators.

Materials and methods

Study site and study species

The study was carried out in the Xishuangbanna Tropical Botanical Garden (XTBG, 101°15′ E, 21°55′ N), located in southwest China and the northern margin of tropical Southeast Asia.

F. glaberrima belongs to the monoecious subsection *Conosycea* and is widely distributed within open forests of mountains and plains of China, Bhutan, India, Indonesia, Myanmar, Nepal, Sikkim, Thailand and Vietnam. Growing up to 15 m tall, populations fruit asynchronously, but each tree produces figs in synchronous crops. Fig size averages 10.4 mm (SD=0.98, n=42) in diameter at maturity. Each fig contains a mixture of female and male flowers. The small numbers of male flowers can be concentrated around the ostiole or scattered amongst the female flowers. Each fig contains 305.29 total flowers (SD=43.53, n=42). The pollinator is an undescribed species of the genus *Eupristina* (Agaonidae). One internally ovipositing non-agaonid fig wasp species (*D. bizarrea*) belongs to Pteromalidae, Sycoecinae. *Eupristina* sp. and *D. bizarrea* are not different lineages. Measure of head width (across the compound eyes), which is a good estimate of the size of the wasps, showed that *D. bizarrea* females are bigger than the pollinator *Eupristina* sp. females (*D. bizarrea* female mean head width=0.32 mm, SD=0.01; *Eupristina* sp. female mean head width=0.30 mm, SD=0.02, n=30; t=−4.73, P< 0.001), so it is essentially impossible that they could be parasitoids. Similarly, the *Diaziella* species studied by Jousselin et al. (2001) was much larger than the pollinators (*Waterstoniella* species) (Jousselin et al. 2001). The anther-to-ovule ratio of *F. glaberrima* is 0.11 (n=42), a ratio which indicates passive pollination by *Eupristina* sp. (Kjellberg et al. 2001).

Collections of naturally growing post-receptive and male floral phase figs

The numbers of *Eupristina* sp. and *D. bizarrea* foundresses inside 60 post-receptive figs (from one tree) were recorded. Fig wasp progeny, together with the numbers of seeds, were also recorded from 51 figs (from two trees) that were collected just before wasp emergence. These figs were placed individually in a fine-mesh bag to allow the fig wasps to emerge prior to counting. The foundress distributions in post-receptive figs and observed fig wasp production (male floral phase figs) are not the same crop and tree.

Experimental introductions of *Eupristina* sp. and *D. bizarrea* foundresses

To ensure that *Eupristina* sp. and *D. bizarrea* successfully entered a fig, their behaviour was observed. In all cases, preliminary observations of adult wasps on three crops of receptive figs (one tree) revealed that *D. bizarrea* and *Eupristina* sp. foundresses always entered each fig on the same day and that *Eupristina* sp. foundresses always entered before *D. bizarrea*. Attempts to experimentally induce *D. bizarrea* foundresses to enter receptive figs that had not been previously entered by *Eupristina* sp., by placing foundresses at the ostiole, were consistently unsuccessful. *D. bizarrea* foundresses could nonetheless be persuaded to enter the ostioles if a *Eupristina* sp. foundress had previously attempted to enter. Based on these observations, we designed the following experiments.

Pre-receptive figs on one tree were enclosed in fine-mesh nylon bags (200×200 mm) to prevent entry and oviposition by fig wasps. Foundresses were obtained from mature figs collected from other trees in the vicinity that were stored in nylon bags until the fig wasps emerged. They were introduced when the figs reached the receptive phase (6.54±0.61 mm in diameter, n=60). To obtain figs entered only by *D. bizarrea* (n=100), one foundress of *Eupristina* sp. was introduced first, but was removed once its head had entered the ostiole. It was then replaced immediately, by a *D. bizarrea* foundress, which was allowed to enter the fig. This procedure was repeated to obtain figs containing both *Eupristina* sp. and *D. bizarrea* foundresses (n=31). In addition, 38 figs that contained only one foundress of *Eupristina* sp. were generated. The mesh bags were then replaced around the experimental figs to prevent access to other fig wasps and were left in place until the figs were nearly mature. After their fig wasps emerged, they were counted, along with the seeds.

Statistical analyses

One-way analysis of variance (ANOVA) was used to compare the number fig wasp progeny and seeds, and t test was used to compare the fig wasp size. All analyses were performed using SPSS (13.0).

Results

Foundress entry into figs

Observations that *Eupristina* sp. and *D. bizarrea* entered receptive phase figs on the same days, but that *D. bizarrea* only entered figs containing *Eupristina* sp. foundresses, were tested. Among the 60 figs (from one tree), 28%

contained only *Eupristina* sp. foundresses, 70% contained both *Eupristina* sp. and *D. bizarrea* and 1.67% (one fig) contained only *D. bizarrea*. Among the 51 mature figs (from two trees), 59% had only *Eupristina* sp. progeny, 41% contained both *Eupristina* sp. and *D. bizarrea* and figs with just *D. bizarrea* were not found. In nature, the post-receptive and mature figs contained only *D. bizarrea* are few (Table 1). The result showed that the occurrence model of *D. bizarrea* and the pollinator *Eupristina* sp. was not random. Adult females *D. bizarrea* preferentially colonise figs that already contain *Eupristina* sp., this result confirms that *D. bizarrea* females do actively seek out figs entered by *Eupristina* sp.

Pollination mode in agaonid wasps

The anther-to-ovule ratio of *F. glaberrima* was low (0.11± 0.02 [mean±SD], n=42 figs from one tree), suggesting that this *Ficus* species is actively pollinated. This was consistent with the anatomy of adult female *Eupristina* sp. (Fig. 1), which have well-defined thoracic pollen pockets (to carry pollen) and coxal combs on their fore coxae (to manipulate pollen). Active pollination by *Eupristina* sp. was confirmed by observation of pollen-loading and pollen-depositing behaviours in mature and receptive figs, respectively.

Can *D. bizarrea* pollinate the figs of *F. glaberrima*?

Under natural conditions, figs containing progeny of both *Eupristina* sp. and *D. bizarrea* produced the same numbers of seeds as those containing *Eupristina* sp. alone (ANOVA, $F_{1,\ 49}$=1.07, P=0.31) (Table 2), but the presence of *D. bizarrea* significantly reduced the abundance of *Eupristina* sp. progeny (ANOVA, $F_{1,\ 49}$=83.62, P<0.001). Experimental introductions of single foundresses into figs of *F. glaberrima* confirmed that *Eupristina* sp. is an effective pollinator of the plant (Table 3). In contrast, all the figs aborted if a lone foundress of *D. bizarrea* was introduced, so no seeds resulted (Table 3). When one *D. bizarrea* foundress was introduced into a fig already entered by a foundress of *Eupristina* sp., seeds and progeny of both species were produced. The presence of *D. bizarrea* in addition to *Eupristina* sp. failed to increase the number of seeds produced ($F_{1,\ 67}$=2.625, P=0.11), but had a significant negative impact on the number of *Eupristina* sp. progeny (ANOVA, $F_{1,\ 67}$=31.86, P<0.001).

Table 1 The frequencies of *Eupristina* sp. and *D. bizarrea* that occurred from figs of *F. glaberrima*

	Post-receptive figs		Mature figs	
	Eupristina sp. present (%)	*Eupristina* sp. absent (%)	*Eupristina* sp. present (%)	*Eupristina* sp. absent (%)
D. bizarrea present	70	1.67	41	0
D. bizarrea absent	28	0	59	0

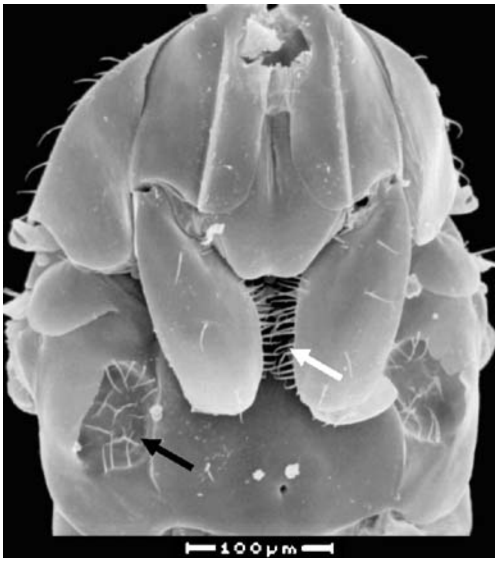

Fig. 1 Ventral views of female *Eupristina* sp. mesosoma. *Black arrow* indicates the pollen pocket and *white arrow* indicates the coxal comb

Discussion

Some non-agaonid fig wasps (*Diaziella* and *Lipothymus* species) that enter figs to oviposit are capable of pollinating them, thereby establishing a mutualism with their host plants (Jousselin et al. 2001; Zhang et al. 2008). In all reported cases, the host plants are nonetheless also associated with a "typical" agaonid pollinator and so are not dependent upon these substitute pollinators. Furthermore, the agaonids are passive pollinators and their host

Table 2 The contents of 51 *F. glaberimma* figs collected from two trees

Model	No. of figs	Seeds (mean±SD)	*Eupristina* sp. progeny (mean±SD)	*D. bizarrea* progeny (mean±SD)
Eupristina sp.	30	107.97±46.99	80.00±19.99	0
Eupristina sp. +*D. bizarrea*	21	96.05±28.46	24.43±23.21	44.71± 24.97

Table 3 The contents of *F. glaberrima* figs with experimental introductions of foundresses

Fig wasp foundresses	No. of figs	*Eupristina* sp. (mean±SD)	*D. bizarrea* (mean±SD)	Seeds (mean±SD)
1 *D. bizarrea*	100	–	0	0
1 *Eupristina* sp.	38	23.39±13.77	–	72.89±29.77
1 *Eupristina* sp.+1 *D. bizarrea*	31	7.48±8.25	7.10±6.81	60.61±33.14

figs have relatively high ratios of anthers to female flowers, produce much more pollen per fig and their mature anthers tend to dehisce naturally facilitating the passive "collection" of pollen by the pollinators (pollen adheres to various parts of the body surface) (Kjellberg et al. 2001). Pollinators of such figs do not require any specific adaptations to achieve effective pollination, so long as foundresses enter figs during their receptive period, which they are forced to do because this is the only time that the ostiolar bracts loosen to form a passage. In contrast, active pollinators, such as the *Eupristina* species associated with *F. glaberrima*, have complex morphological and behavioural adaptations that ensure that the relatively small amounts of pollen available to them can be collected and transferred. Such behaviour has been shown to benefit foundresses by increasing the survivorship of their larvae (Jousselin et al. 2003; Tarachai et al. 2008; Herre et al. 2009). It is important to note that the basal condition of figs and their pollinating wasps is passive pollination (Machado et al. 2001; Herre et al. 2009). Thus, the behavioural characteristics in the wasps and the morphological characteristics in the figs that are essential for active pollination can be acquired during the course of co-evolution.

Consistent with the predictions of Jousselin et al. (2001), our study failed to detect any evidence that *D. bizarrea* contributes to the pollination of *F. glaberrima*. *D. bizarrea* was incapable of developing in figs unless they also contained the agaonid *Eupristina* sp. Furthermore, the experimental introduction of *D. bizarrea* foundresses into figs failed either to produce seeds when the *D. bizarrea* females were introduced by themselves (the figs were aborted) or to increase seed production when there were pollinator foundresses also introduced into the fig. Furthermore, because *D. bizarrea* foundresses reduced the number of *Eupristina* sp. progeny produced, they have a negative impact on the mutualism. Using control experiments, we found a negative relationship between the pollinator and *Diaziella* species, but the number of *Diaziella* species progeny was not correlated with the number of seeds. In contrast, using non-experimental data, Jousselin et al. (2001) concluded that the number of the pollinator progeny was not correlated with the number of *Diaziella* progeny, and *Diaziella* species can transport more pollen than the pollinator. The discrepancy between the two studies could be due either to the greater power of an experiment (our study) to resolve real differences or because of real biological and ecological differences between the study systems. The contrast between these results and those of Jousselin et al. (2001) and Zhang et al. (2008) confirms that the ability of non-agaonids to act as substitute pollinators is dependent of the mode of pollination of their associated agaonid fig wasps. Specialised active pollination behaviour, as seen in agaonids, has not been observed amongst non-agaonids, making them incapable of actively pollinating figs species that do not produce large amounts of pollen.

Such complex behaviour can be lost as well as gained. The African agaonid *Ceratosolen galili* is exceptional in that it fails to pollinate its host figs, yet retains anatomical adaptations associated with pollen collection and transport. Its relationship with its actively pollinated host fig tree (*F. sycomorus*) is largely analogous to that between *D. bizarrea* and *F. glaberrima*, in that *C. galili* does not routinely transport pollen and, in shared figs, reduces the abundance of the legitimate pollinator. A few pollen grains may nonetheless be transported and, on rare occasions, this may result in seeds being produced (Compton et al. 1991). *C. galili* nonetheless differs from *D. bizarrea* in one major aspect of its relationship with its host plant, as it is capable of developing in figs that have not been entered by the tree's legitimate pollinator, *C. arabicus*. It is interesting to note that, recently, a second known case was discovered in which an active pollinator species has lost its capacity to pollinate the host and effectively become an internal parasite. In southern China, the fig *Ficus altissima*, which is pollinated by *Eupristina altissima*, also has a *Eupristina* sp. associated with it that has lost the capacity to pollinate (Peng et al. 2008).

For an internally ovipositing species like *D. bizarrea* with foundresses that lose their wings when entering a fig and rarely re-emerge, this lack of independence would appear to be hazardous, but the risks are reduced by the wasps' behaviour. Foundresses enter the figs later in the day than do the pollinators, the time interval between these activities ranged from less than 1 min to 6 h, and they are unwilling to enter figs that have not had a *Eupristina* sp. foundress. The nature of the cue left by the agaonids is unclear, but it cannot be their wings. The nature of this signal is certainly chemical.

The precise nature of the ecological relationship between *D. bizarrea* and its associated pollinator remains unclear.

The presence of a *D. bizarrea* foundress reduced the number of progeny produced by a *Eupristina* sp. foundress sharing the same fig, but this could have resulted from interference between the two foundresses (leading to less *Eupristina* sp. eggs being laid), competition between the foundresses for a limited number of oviposition sites or from *D. bizarrea* acting as a parasitoid/inquiline and killing *Eupristina* sp. larvae. Our results have shown that, where careful experimental studies have been conducted, *Diaziella* species are completely dependent on the pollinator for its own development (at least in *Ficus curtipes* and *F. glaberrima*), it directly parasites (a parasitoid of) the pollinator or it depends on some aspect of the pollinators influence in order to develop itself. Now *Diaziella* species is physically bigger than the pollinator, so it is unlikely to be a direct parasitoid. So it somehow depends on the pollinator to induce a gall or the pollinator is able to initiate a gall in a particular flower that the *Diaziella* species can then take over (same flower) or there is some more general influence that allows the fig to "accept" the gall formed by the *Diaziella*.

The natural history of internally ovipositing non-agaonid and agaonid wasps fig wasps has been thought to be largely similar with both having larvae that develop in ovules that are galled by foundresses at the same time as oviposition takes place (Galil and Eisikowitch 1969, 1970). This raises the question of why non-agaonids have failed to evolve independent mutualistic relationships with their host figs (Herre 1999; Jousselin et al. 2001; Zhang et al. 2008; Herre et al. 2009). Based on the results presented in this study, it appears that the development of an independent mutualism between fig trees and non-agaonids would require the following combination of factors: (1) an internally ovipositing fig wasp (2) associated with a passively pollinated host *Ficus* that (3) can develop in ovules that it has galled and (4) has the ability to prevent the figs that it occupies from being aborted by its host plant. Alternatively, the internal non-pollinator would have to acquire active pollination morphology and behaviours, as well as go through similar steps in actively pollinated figs.

Some internally ovipositing non-agaonids are capable of developing independently from their pollinator fig wasps as they can both gall individual ovaries and prevent the figs from aborting. They include at least some species of the African genera *Sycophaga* (Sycophaginae) and *Philocaenus* (Sycoecinae) (Galil and Eisikowitch 1970; S. Compton, unpublished). However, the agaonids associated with these species are active pollinators; so, like *D. bizarrea*, these non-agaonids rarely, if ever, transport pollen (Compton et al. 1991). Conversely, species such as *D. yangi* and *Lipothymus* sp. are effective pollinators of the passively pollinated *F. curtipes*, but they can only develop in figs shared with the tree's agaonid pollinator (Zhang et al. 2008). To date, a different *Lipothymus* sp. and its host *F. consociata* in Brunei remain the only possible example of a fig tree with an independent non-agaonid pollinator. This *Lipothymus* was reared from *F. consociata* figs that lacked progeny of its associated agaonid (*Waterstoniella malayana*) and these figs contained just as many seeds as those that produced *W. malayana* (Jousselin et al. 2001); this case needs to be studied more carefully using controlled experiments such as we have used in this study.

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