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ORIGINAL PAPER

Coordinating a group departure: who produces the piping signals on honeybee swarms?

P. Kirk Visscher · Thomas D. Seeley

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Abstract A swarm of honeybees provides a striking example of an animal group performing a synchronized departure for a new location; in this case, thousands of bees taking off at once to fly to a new home. However, the means by which this is achieved remain unclear. Shortly before takeoff, one hears a crescendo of a high-pitched mechanical signal—worker piping—so we explored the role of this signal in coordinating a swarm's mass takeoff. Specifically, we examined whether exclusively nest site scouts produce the worker piping signal or whether it is produced in a relay or chain reaction fashion. We found no evidence that bees other than the scouts that have visited the swarm's chosen nest site produce piping signals. This absence of relay communication in piping suggests that it is a signal that only primes swarms for takeoff and that the release of takeoff is triggered by some other signal or cue; perhaps the takeoff of bees on the swarm periphery as they reach flight temperature in response to piping.

Keywords *Apis mellifera* · Decision-making · Group movement · Piping · Positive feedback

Introduction

Animals that move about in cohesive groups must possess mechanisms of social coordination that enable them to start and stop their movements in unison. In some cases, the mechanism is despotic, i.e., one dominant individual decides and directs the others; while in others it is democratic, i.e., a majority of group members decides (Conradt and Roper 2003). Examples of species with despotic mechanisms include hamadryas baboons (*Papio hamadryas*) where the exaggerated swagger of an old male is able to precipitate a band's morning departure (Kummer 1968) and African elephants (*Loxodonta africana*) where an adult female will lift one leg and repeatedly give long "let's go" rumbles accompanied by steady ear flapping to incite a stationary group to move off together (Poole et al. 1988). Examples of species with democratic mechanisms include gorillas (*Gorilla gorilla*) where calling by a majority of a group's adults signals an impending departure (Stewart and Harcourt 1994) and whooper swans (*Cygnus cygnus*) where a group takes off when the intensity of head movement signals reaches a threshold level (Black 1988).

Social insect colonies show a high degree of group integration and provide many examples of groups moving as cohesive units (reviewed by Dyer 2000). A vast literature has developed concerning the mechanisms underlying group integration and collective action in social insects (Camazine et al. 2001), but the mechanisms mediating the initiation of their group movements remain poorly studied. The most extensive information is for the honeybee (*Apis mellifera*), but even for honeybees, we do not know what coordinates this takeoff and what underlies its explosive, all-at-once nature.

A clustered swarm of honeybees looks like a fuzzy bundle hanging in a tree. For a few days, this mass of insects remains largely quiescent with just occasional comings and goings of the scout bees searching for a new home site and dances of these bees on the swarm surface recruiting other scouts to their finds. But suddenly, within a few seconds, all

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P. K. Visscher (✉)
Department of Entomology, University of California,
Riverside, CA 92521, USA
e-mail: visscher@ucr.edu

T. D. Seeley
Department of Neurobiology and Behavior, Cornell University,
Ithaca, NY 14853, USA

the tens of thousands of bees that had remained quietly clustered take off into the air.

We know that the shift in behavior from quietly clustered to airborne swarm involves a number of signals and a series of behaviors. First is the waggle dance with which successful nest site scouts inform others of the direction and distance to potential nest cavities (Lindauer 1955; Visscher 2007). The better the potential nest site, the greater the number of waggle runs produced by a scout when she returns to the swarm cluster and the larger the stream of fellow scouts to the site. The result is a growing number of scout bees at favored sites. The presence of other bees at the site appears itself to be a signal because the decision of when to shift from simply recruiting to preparing the swarm for takeoff is based on sensing that a quorum of scouts is visiting the nest site (Pratt et al. 2002; Seeley and Visscher 2003, 2004). Once a quorum is reached at the chosen site, some bees at the swarm cluster begin generating piping signals, which are produced by a bee pressing her thorax against another bee and vibrating her wing muscles to produce a 0.85 s "motor-revving" sound, whose fundamental frequency sweeps upward from 180 to about 250 Hz (Seeley and Tautz 2001). This mechanical signal causes other bees in the swarm cluster to begin to warm up, also by activating their wing muscles, but not audibly. When all of the bees in the cluster have achieved a thorax temperature of at least 35°C, the swarm is ready for takeoff and takeoff usually follows a minute or two later (Seeley et al. 2003), perhaps in response to other, not-yet-identified signals.

There are two kinds of mechanisms that could account for the explosive nature of swarm takeoff. One of these, suggested by Wilson (1971, p. 270) would be for it to be based on some kind of signal in which positive feedback occurs with bees that receive the signal producing it themselves in a chain reaction that grows exponentially, thus leading to a sudden and widespread propagation of the signal so that all individuals experience a threshold level of the signal in a short time window. An alternative mechanism would be one where there is a primer and releaser. This would involve a priming signal or signals, which, over the course of a shorter or longer period, are perceived by all of the bees on the swarm and that shift them into a state of readiness and attention. Then some other signal or signals could serve as a releaser if they were either perceivable throughout the swarm simultaneously or rapidly propagated in some manner.

Donahoe et al. (2003) argue that the vibration signal in which a bee grasps another with her feet and shakes her body dorsoventrally, serves as a modulatory or primer signal, making bees more responsive to other signals. It seems clear, however, that the vibration signal does not release swarm takeoff because it is produced throughout the house-hunting process and its production declines shortly before takeoff. Lindauer (1955) described bees on the swarm performing buzz-runs (*Schwirrlaufen*) in which a bee runs in a zigzag pattern, buzzing her wings, butting into other workers, and vigorously forcing her way into and through the swarm cluster. Buzz-running increases a few minutes before swarm takeoff (Lindauer 1955; Camazine et al. 1999) and so could serve as a releaser signal.

The piping signal on swarms seemed a candidate for a signal where there might be a positive feedback/chain reaction. Certainly, the level of piping rises to a crescendo just before swarm takeoff. We knew from previous observations that at least some of the piping is performed by nest site scouts because focal sampling of pipers had revealed that piping is often interspersed with waggle dancing (Seeley and Tautz 2001). However, we did not know whether the key aspect of relay communication occurred, i.e., whether bees that had not visited the chosen site passed on the signal after receiving it. This study was performed to clarify this issue. Our approach was to present swarms, one at a time with a nest box that they would choose for their new home, mark the scout bees that visited this nest box, and observe at the swarm cluster what fraction of the piping bees were marked nest box scouts. If there is relay communication producing positive feedback among the piping bees, then many of the pipers should be unmarked bees rather than marked nest box scouts. But if there is no relay communication, then all of the pipers should be marked nest box scouts.

Materials and methods

Study site and experimental setup

To mark the scouts visiting a particular nest site requires control over the nest sites available to a swarm. To achieve this control, we offered an attractive nest box to swarms of bees that we took to Appledore Island, a 39 ha island off the coast of Maine (42°58′N, 70°37′W) where there are no trees large enough to contain potential nest cavities and where few other suitable nest sites can be found by bees.

The swarms we used were artificial swarms, prepared by shaking 1.1 kg, about 8,000 individuals bees, from the combs of a hive into a screen cage with their queen in a smaller cage among them, then feeding this cage of bees with sucrose solution (1:1 sucrose:water by volume) for 3 days. The production of abundant wax scales signified that these bees had shifted into a condition like that of a natural swarm, and we then set them up on a stand for observation. The swarm stand was that described by Seeley and Buhrman (1999), except we did not include the mesh dance floor they described. This stand spread the swarm out over one surface of a board, so that activities on the surface could be more easily monitored.

We set up each swarm, one at a time, on a porch of the old Coast Guard building, and placed a 40-l nest box with a 12.5 cm^2 entrance hole, like that described by Seeley and Morse (1978) at a distance of 255 m from the swarm. The nest box, which has the characteristics favored as a home site by bees, was sheltered in a small hut and placed in a direction in which there are no buildings on the island to help distinguish dances for it from dances for other nest sites the bees might find.

Scout marking

One of us (PKV) then waited at the nest box for scout bees to arrive. When a scout arrived, she was caught in a 15-cm diameter, 40-cm deep insect net, either by placing it over the nest box entrance while the bee was inside or by catching her in flight. The bee was then marked with a spot of shellac-based paint (von Frisch 1967) on her thorax, while trapped in the net, and then released either into the nest box, through its entrance, when scout activity permitted, or just outside when many scouts were present. A tally was kept of the number of scouts marked during each 10 min interval from first discovery to takeoff of the swarm. Although we planned to mark every scout that visited the nest box, when many scouts came it was not always possible to catch and mark every one. To estimate the proportion of the scout bees that returned to the swarm unmarked, we netted samples of bees exiting the nest box or flying near the entrance and counted the marked and unmarked bees in these samples. These censuses were done about four times per hour; they tended to overestimate the proportion of scouts that returned to the swarm without being marked. This is because each scout entered and exited the nest box numerous times, hence she provided multiple opportunities to be caught and marked. As a result, some of the unmarked scouts in a census would ultimately be marked before they returned to the swarm.

Swarm observations

Meanwhile, at the swarm cluster, one of us (TDS) observed and videotaped the activities of the bees on the swarm surface. If a bee danced in a direction that indicated a site other than our nest box, she was removed from the swarm to prevent buildup of scouting to unmonitored sites. However, our first swarm located a nest site close to the direction of the nest box. Because radio failure prevented communication between observers at the nest box and the swarm, we allowed scouting to build up for this unmonitored site and the swarm selected it and took off to move to it; though during the same time period scouts discovered and recruited to, and were marked at, the monitored nest box. This accident, though, proved highly informative.

To identify pipers on the swarm, a small electric condenser microphone (Radio Shack Model 33-3013, 70–16,000 Hz frequency response) was plugged into the video camera (Sony DCR-TRV50) and its output was monitored through headphones. A 40 mm length of 8 mm internal diameter Tygon tubing was attached to the microphone to make it directional. When piping began on the swarm, it could be heard through the microphone and moving the microphone close to individual bees on the swarm cluster's surface made it possible to positively identify which of these bees were producing piping signals. We located pipers with a scan sampling procedure: starting at the top of the swarm, a series of horizontal left to right passes were made, visually and with the microphone, to the bottom of the swarm, and then repeated. Each piping bee was announced as marked or unmarked, for later transcription from the videotape audio track. Because many bees may pipe at once, and because piping bees move between the surface and interior of the swarm cluster, we were able to identify only a subset of the bees that piped, but we are confident that our subset was a random sample of all pipers.

Transcription and analysis

We played back the videotapes of each swarm and noted each instance of identifying a piping bee, the time at which this occurred, and whether the bee bore a paint mark indicating that she had visited the nest box. To graph an estimate of the cumulative number of scouts (marked and unmarked) that had visited the nest box for each 10-min time period, we divided the cumulative number of scouts that had been marked by the proportion of marked scouts in the censuses performed within 30 min of that 10-time period.

We performed a chi-squared test for homogeneity to see if the counts of marked and unmarked pipers and the census counts of marked and unmarked nest site scouts, taken during the period when piping was occurring, were consistent with them being drawn at random from the same population. The relay communication hypothesis predicts that the proportion of marked pipers will be markedly *smaller* than the proportion of marked scouts because many of the pipers will be unmarked bees that never scouted the nest box. The no-relay-communication hypothesis predicts that the proportion of marked pipers will be the *same* as or even *greater* than the proportion of marked scouts (because, as explained above, we probably overestimated the proportion of unmarked scouts).

Results

Figure 1 shows, for each of the three swarms studied, the time course of scouting as the cumulative number of scouts

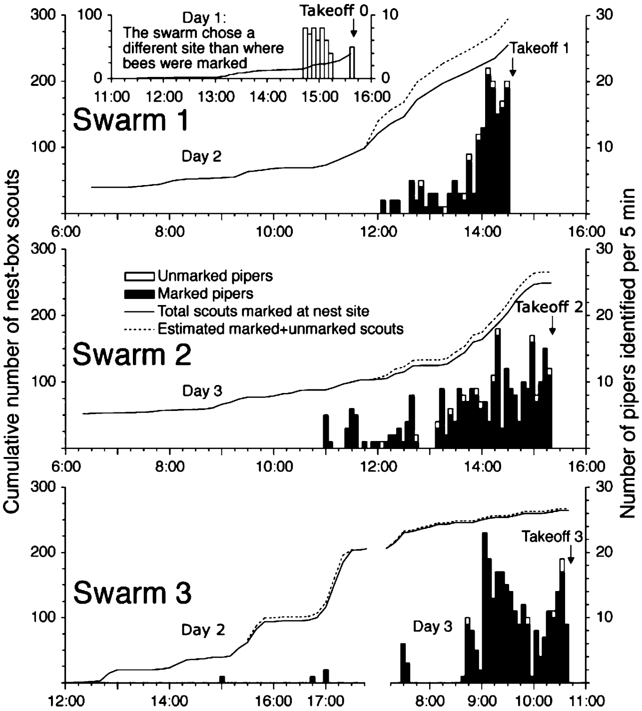

Fig. 1 Time course of nest box scouting and piping on three swarms. Scouting is represented by the *solid line* (and *left axis*) showing the cumulative number of scouts marked. The *dotted line* represents an estimate of the total number of scouts that visited the nest box, including ones that escaped marking on their visit(s) to the nest box. The number of bees seen piping during each 5-min interval is shown by the *histogram bars* (and *right axis*); marked pipers are in *black* and unmarked ones are in *white*. The *inset* in swarm 1 shows scouting of the nest box and piping by this swarm during a buildup and takeoff to a different, unmonitored site

marked at the nest box; the rate of arrival of new scouts is the slope of the lines. It also shows the buildup of piping leading to takeoff for each swarm. Except when the swarm was making preparations for takeoff to a different site than the nest box (Fig. 1, swarm 1, inset), nearly all of the piping bees were marked nest box scouts (Fig. 1; Table 1). In the three trials in which the swarm was preparing to take off to our nest box, the proportion of marked pipers was never significantly less than would be expected from the proportion of marked nest box scouts (Table 1).

Swarm 1

We set up the first swarm at 11:00 on June 15, 2006; it discovered our nest box by 11:45 and a slow buildup of scouts followed there (Fig. 1, swarm 1, inset). However, the bees discovered another attractive site in approximately the direction of the nest box about 13:30, and apparently rapidly recruited to it, so that piping began at 14:30. The piping was performed entirely by unmarked bees, even though all bees that visited the nest box were marked. A thunderstorm interrupted the process at 15:10, but after it passed, piping began again, quickly followed by takeoff of the swarm, which then returned to their caged queen on the swarm stand. On day 2 (Fig. 1, swarm 1), we removed many dancers for the unmonitored site early in the day, and scouting built up for our nest box, leading to piping and takeoff in the afternoon. The number of new scout arrivals exceeded our ability to mark them all; we estimated that 87% of the scouts that visited the nest box were marked. The proportion of marked pipers was significantly greater than our estimate of the proportion of nest box scouts that were marked (Table 1).

Swarm 2

Swarm 2 was set up at 14:00 on June 19, 2006; a windy day. It discovered the nest box only late in the day with little recruitment. Day 2 was also windy. There was very little dancing for any nest sites; only 20 scouts had visited the nest box with never enough number to constitute a quorum there at once, but nonetheless the bees began to pipe (not shown in Fig. 1). This piping led to takeoff of the swarm and the beginning of flight in a direction opposite the nest box. However, the bees returned to the swarm stand because their queen was caged there, and resumed scouting the nest box. On day 3 (Fig. 1, swarm 2), there was gradual buildup until piping began at 11:00, but then died back around 12:45, probably because of cool weather. Piping resumed after 13:00 and built up to takeoff late in the day. With this swarm, we were able to mark an

Table 1 Comparisons of the proportion of scout bees at the nest box that were marked and the proportion of piping bees at the swarm cluster that were marked

Swarm (takeoff #)	Nest box scouts			Piping bees			Chi-square	*P* value
	Marked	Unmarked	Percent marked	Marked	Unmarked	Percent marked		
Swarm 1 (1st)	39	0	100	0	52	0	91	≪0.001
Swarm 1 (2nd)	138	21	87	163	9	95	6.38	<0.05
Swarm 2	272	18	94	266	12	96	1.01	0.32 NS
Swarm 3	96	1	99	274	5	98	0.27	0.61 NS

The nest box scout counts are the totals of censuses taken after piping began on each swarm. In swarm 1's first takeoff, there was dancing and, ultimately, takeoff for a different site than the nest box. Note that in swarm 1's second takeoff, the proportion of marked pipers was significantly different from, but greater than, the proportion of marked scouts.

estimated 94% of the bees that visited the nest box. The proportions of marked nest box scouts and marked piping bees matched closely (Table 1).

Swarm 3

We set up swarm 3 at noon on June 26, 2006, but cloudy weather resulted in little activity from the swarm for the rest of the afternoon and the next morning. The bees discovered the nest box just after noon on day 2, and a strong buildup of scouts occurred during the late afternoon, but there was no piping, in spite of the numbers of bees at the nest box that would normally satisfy the bees' quorum. The next morning (day 3), there was strong scouting and some early piping. This waned as the sky clouded and became foggy, but then picked up again after 08:30 when the sun returned. Twice during the rest of the morning, piping dropped off when the weather cooled (Fig. 1, swarm 3), although scouts steadily visited the nest box. These scouts also danced regularly up until the swarm took off in late morning, but relatively few unmarked bees (recruits) arrived at the nest site, perhaps because more than 250 bees already marked comprised most of the swarm's scouting force. With this swarm, we were able to mark an estimated 99% of the bees that visited the nest box. Once again, the proportions of marked nest box scouts and marked piping bees matched closely (Table 1).

Discussion

The conditions under which bees produce piping signals

The results of this study include two examples demonstrating that the usual association of piping with nest site scouting and dancing is not absolute. Piping can occur without dancing and scout buildup, and dancing and scout buildup do not necessarily lead to piping. Swarm 2 bees piped on their second day despite very little dancing after an afternoon and then a morning of cold and windy weather, and this led to takeoff of the swarm. On one other occasion in previous studies, we observed a similar takeoff without much dancing or scouting activity. Because the queen was caged in both instances, we could not tell where the swarms would have gone, but we suggest that in each case the swarm was attempting to move its cluster to a more protected site, not a nest cavity. This rare behavior poses interesting puzzles in terms of which bees initiate the process of swarm relocation, whether a specific new clustering site had been selected, and how the movement there would be coordinated after takeoff. Perhaps conditions can be manipulated to reproducibly induce this cluster-relocation behavior, but at this point there is no information regarding these puzzles.

The behavior of swarm 3 (Fig. 1) is of particular interest with regard to the conditions under which scout bees produce piping signals. On day 2, there was intense recruitment to the nest box late in the day. The number of scouts that had been marked at the box exceeded 200 and the number present at any one time was as great as we had seen in previous swarms when piping began, yet there was virtually *no piping*! This indicates that while a quorum at the chosen nest site is usually necessary to induce scouts to pipe on their return to the swarm cluster, it is not sufficient. In this case, the late hour may have inhibited piping. Furthermore, on day 3, we observed that visitation to the nest box remained high throughout the morning, but piping dropped off several times when the weather became cloudy or foggy. These observations suggest that in making the decision to pipe, scout bees assess the conditions and only pipe when there is an opportunity to make a safe flight, not just the presence of the nest site quorum. This is similar to the decision of a successful forager to dance, which is influenced by the time of day and the weather, not just the desirability of her food source (von Frisch 1967; Seeley 1995).

Which bees produce piping signals

Aside from the cluster-relocation liftoff just discussed, the results of this study suggest strongly that *piping is only performed by scout bees that have themselves been to the chosen nest site*. In all three cases when the swarm was preparing to fly to the nest box, the proportion of pipers that were marked matched or exceeded the proportion of nest box scouts that were marked. Indeed, we never saw more than a few unmarked pipers, except in the first takeoff by swarm 1 when the bees were preparing to fly to a site other than our nest box. These results strongly contradict the relay-communication hypothesis and support the no-relay-communication hypothesis. As previously observed (Seeley and Visscher 2003, 2004), piping began only after the number of scouts at the nest site reached a fairly high level—the quorum. The results from the first takeoff of swarm 1 in which the marked bees were nest site scouts, but were not scouting the chosen nest site and did not pipe, suggest that to become a piper, a bee must not only be a nest site scout, but must also have experienced quorum-level activity at her nest site. Together, these observations suggest that a scout bee that visits the chosen nest site and experiences a quorum-threshold level of other scout bees there, through still unknown mechanisms, is likely to pipe when she returns to the swarm, but other bees on the swarm, whether nest site scouts or not, do not pass on the signal.

This is sensible. One of the salient characteristics of a swarm's decision-making process is the independence of the scout bees at each phase of the process: initial discovery and assessment, and then reassessment by each scout. Within this decision-making process, relay communication in any form would be like a rumor spreading in human society: liable to disperse misinformation. There is great variance in the dance responses of individual bees to any one nest site; while many bees will dance only briefly for a mediocre site, others will dance extensively and still others won't dance at all. This variation among individuals in dancing may reflect differences in the bees' evaluations of the site or perhaps differences in their individual thresholds for dance response. Either way, the collective intelligence of a swarm's nest site selection relies on the pooling of many bees' independent assessments of nest site quality. Although a difference among bees in response to a given number of other scouts at the nest site has not been documented, it undoubtedly occurs. The shift from dancing to piping is not precipitous for all scouts, and after a quorum level of scouts builds up, piping continues to increase as the scout numbers increase further. If relay communication in piping were the rule, scouts that had erroneously sensed a quorum could set off a flurry of piping prematurely.

Primers and releasers in takeoff

Our results suggest that the explosive takeoff of a honeybee swarm is not caused by positive feedback in the production of piping. Instead, it seems likely that piping plays only a priming role. This role may be exclusively to get the bees of the swarm warmed up to the point at which they are ready for flight. It would be of interest, therefore, to know whether piping occurs or whether its time course is abbreviated when the bees do not need to warm up for flight, i.e., at high environmental temperatures.

If piping plays a priming role in a primer–releaser system, then what is the releaser? Is there some other signal working by the positive feedback mechanism? No specific signal has been identified that is unique to the time immediately before swarm takeoff. Because piping commonly increases up to takeoff, a certain threshold level of piping could serve as a takeoff releaser. However, our results argue against this (see especially Fig. 1, swarm 3) because the level of piping, estimated from the number of piping bees encountered per time in continuous scans, is not always highest just before takeoff. Buzz-running, although it does occur at the nest site and the swarm throughout the warm-up process, is much stronger on the swarm in the minutes before takeoff (Lindauer 1955; Camazine et al. 1999) and might contribute to releasing swarm takeoff.

An intriguing possibility is that the releaser of takeoff is, in a sense, takeoff itself. Swarms usually take off very shortly after the outermost bees reach a thoracic temperature suitable for rapid flight, about 35°C (Seeley et al. 2003). However, by the time this occurs, the swarm has already become noticeably more fluid and less densely clustered, probably through the actions of piping and buzz-running bees. It may be that in this primed state, bees are sensitive to whether other bees are on top of them. When the outermost bees can fly, they do, and this in turn makes the next-lower bees outermost, and they, being ready, fly too. This would meet the expectation of a release signal that propagated very rapidly within the cluster and it would help explain how takeoff is coordinated as a nearly simultaneous activation of tens of thousands of bees. However, this mechanism remains speculative. It may be that there is no single releaser signal and that takeoff involves both a priming and activation by piping signals and perhaps vibration signals (Donahoe et al. 2003) and a release by an interaction of multiple signals. The 100 or so seconds immediately preceding and during takeoff invite more scrutiny.

The simultaneous activation of tens of thousands of individual honeybees into coordinated movement as a flying swarm does not rely on any single individual dictating the moment of departure, as in the movement of a troop of baboons or a herd of elephants. However, only a small minority of the bees is active in producing the signals indicating the time of departure. This study clarifies that one of the signals important in swarm takeoff—piping—is confined to scout bees that have visited the chosen nest site. The decision by this "committee" of scout bees that it is time to take flight is apparently communicated in a two-step process in which the swarm is first primed for flight and then released into flight. This is quite similar to the democratic situation in whooper swans where a signal is built up with increasing group-wide activity. The complexity of the honeybee system with multiple signals interacting, probably reflects that no single individual can know whether the criterion for takeoff, a consensus with sufficient scouts at a good nest site, has been achieved. The need for multiple signals from multiple individuals and the absence of relay communication in these signals (at least, as shown here, in the piping signal) may serve as a check on premature action. Such mechanisms may be common in very large groups where single individuals cannot simultaneously communicate with the entire group, as is commonly the case in social insect colonies.

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