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Taking the Sting out of Wasp Nests: A Dialogue on Modeling in Mathematical Biology

Jennifer C. Klein and Thomas Q. Sibley



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This dialogue fancifully reconstructs the first modeling project in our Mathematical Biology class.

Dramatis Personae:

Sophia—a mathematical biologist

Vespa—an entomologist

Quint—a *quintessential* mathematician

[Sophia and Vespa meet in the faculty lounge. We join them after some small talk.]

Sophia: Vespa, my friend, do you have any intriguing questions to tempt a mathematician?

Vespa: If you are looking for a challenge, my own research has encountered a snag. Have you noticed, Sophia, the nearly round shape of the wasp nests here in Minnesota? It intrigues me that nests of tropical species are almost always quite elongated, even though they're built from the same hexagonal unit cells. [See Figure 1.] I am curious: Can evolution explain such differences?

S: As a biologist, you probably have many possible conjectures for the differences you've observed, but I don't see where mathematics could be of any use.

V: As is generally the case, I'm afraid I have more hypotheses than mathematicians have hypotenuses. Nevertheless, you can help me investigate one plausible explanation. I suspect that wasps in temperate climates find significant selective advantage building round nests because these nests require the least materials or energy. However, to measure how close they come to optimal I need a straightforward way to quantify the cost of different shaped nests. Also, for comparison I need the cost of the most efficient arrangement for any number of cells.

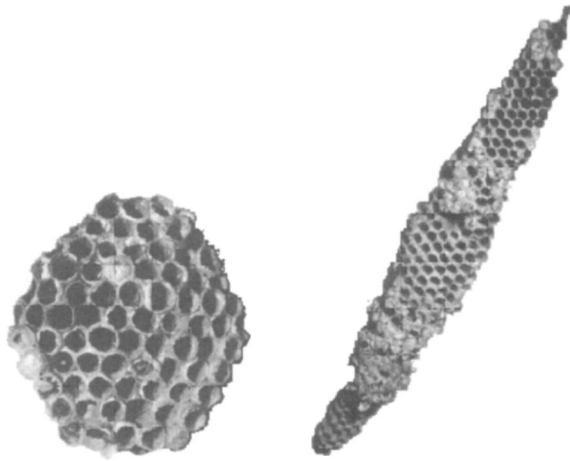


Figure 1.

S: Let's start with the number of cells in the nest and consider different arrangements of cells. We could then

V: And we can ignore for our purposes the hive-like covering of the nests some species build. But I'm not sure we can ignore such imperative factors as predation and climate. For example,

S: Vespa, I hate to interrupt

V: Ants are serious predators in the tropics and an elongated nest confers an important advantage. Ants can enter an elongated nest only along a narrow, easily guarded twig compared with the larger surface area a circular nest offers an ant dropping down on it. Further this twig can be effectively covered in ant-repelling secretions. [Vespa insists that Sophia feel the dried black goo at the end of such a nest.]

S: That's, umm, very nice Vespa, [Sophia quickly sets the nest aside and sits down] but we must remember to keep things simple. Predation and other environmental factors are clearly important, but you surely don't expect a mathematical model to tell you about ant control. Let's postpone these questions until later.

V: I suppose so. Where did we leave off?

S: The number of cells seems to determine the amount of material forming the base of the cells, regardless of how they are arranged. So as a first approximation any differences in costs between arrangements can be attributed to the number of cell walls in a nest.

V: Yes, that is what I decided—and the number of walls varies quite noticeably with nest shape. However, nests can have well over a hundred cells and so hundreds of walls. I've counted walls for various nests, but it is slow, tedious work and prone to errors, I can assure you. There has to be an easier way to count these exactly or else I'll never coax enough students to do all the counting I need for publications.

S: Let's look at some small examples. Figure 2 shows some diagrammed nests together with the values of n , the number of cells; w , the number of walls; and some other values that might prove useful: n_e , the number of exterior cells; w_e , the number of exterior walls; and w_i , the number of interior walls.

[Quint wanders in holding a coffee cup.]

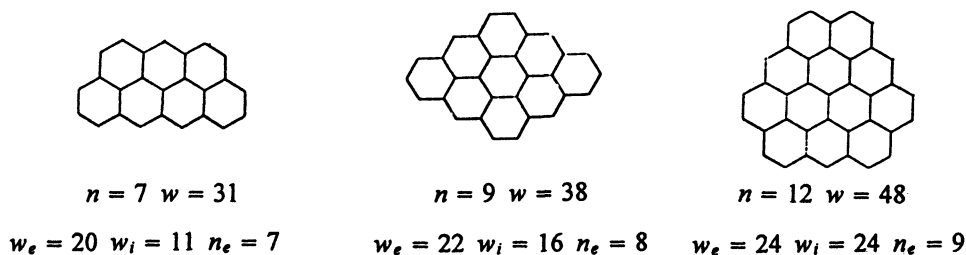


Figure 2.

V: Hey there, Quint. Do you suppose we could distract you from your hunt for caffeine for a bit?

Quint: Hello, Sophia, Vespa. What are these numbers and figures you are so intently studying?

S: Hi, Quint. I'm helping Vespa work on

Q: Oh, I know Vespa—always buzzing on about insects. Don't bug me with entomology or etymology or whatever you call it; just get to the good stuff. You seem to be counting. [Quint sits next to Sophia, immediately absorbed in the examples.]

S: Vespa suspects that round nests use close to the minimum number of walls for a given number of cells. However, counting walls is boring and inaccurate, so he wants a nice way to find the number of walls from the number of cells. It is much easier to count the number of cells.

Q: Let's see. Obviously, $w = w_e + w_i$. Since these cells, as you call them, all have six edges—no, you call them walls—there are potentially $6n$ walls, but the interior walls count for two cells. So $6n = w_e + 2w_i$. A little algebra gives $w = 6n - w_i$ or $w = 3n + w_e/2$. Both of those avoid counting some of the walls.

S: Yes, I see your equations, but we want to avoid the walls altogether. Notice in these examples how w_e goes up 2 each time n_e goes up 1. That would give $w_e = 2n_e + 6$. From your last equation we can conjecture $w = 3n + n_e + 3$.

V: Nice formula. It will cut the tedium a lot. Thanks.

Q: Not so fast. That looks good—too good. How about the examples in Figure 3? Here that formula of yours falls apart. Nice try, but one counter-example ruins a conjecture in math.

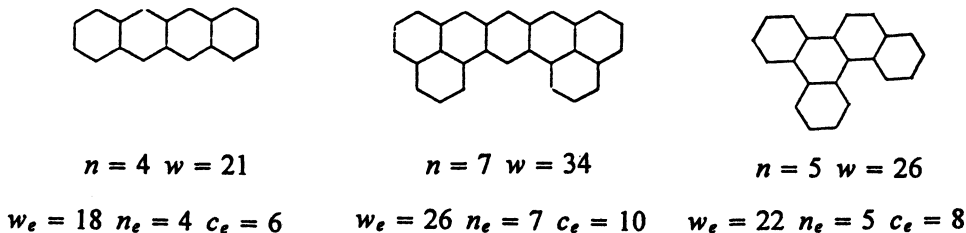


Figure 3.

V: Well, some wasp nests are only one cell thick in places, although not consistently that thin: they wouldn't hold together all that well. Maybe these exceptions don't matter—I don't want to lose such a lovely formula. [Vespa sighs.] I really want to avoid counting walls!

S: And you shall. We just need to count exterior cells so that our formula holds for these examples as well.

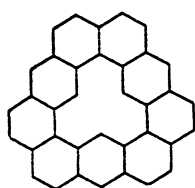
Q: I always suspected that you mathematical biology types played loose with proofs, but I never would have guessed that you go in for “creative accounting.” Next thing I know, you’ll offer to do my taxes.

S: Oh! I see a pattern. Suppose that we count how many of these exterior cells we encounter in a circuit. Pick any outside cell and start the count at 1. As we come to succeeding exterior cells, raise the count by 1 until we get back. With a nice nest, this gives n_e , but with these thin nests, a cell will be counted more than once *and* we get the right number. Yes! Let’s call this number c_e . So our formula is $w = 3n + c_e + 3$.

V: Well, that is creative! I guess I could take your word that this always works.

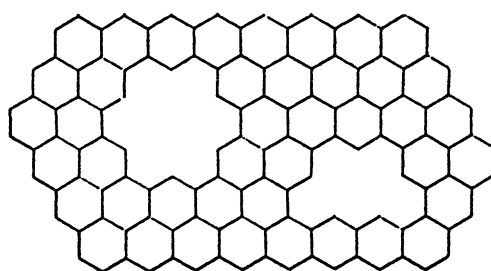
S: No, once we have a formula that we think is correct for all nests we do need a proof.

Q: All nests, you say? Well, how about the ones in Figure 4? Even your creative counting won’t survive these examples.



$$n = 9 \quad w = 45 \quad c_e = 9?$$

$$(m_1 = c_1 = 3 \quad h = 1)$$



$$n = 42 \quad w = 170 \quad c_e = 24?$$

$$(m_1 = 7 \quad c_1 = 6 \quad m_2 = c_2 = 5 \quad h = 2)$$

Figure 4.

S: [disappointed] Oh!

V: But really, now. Wasps don’t build nests with holes in them. I don’t care if our formula doesn’t work for “holey” nests as long as it works for real ones.

S: All right. Assume nests without holes. What can we do with that?

Q: Humph. Clearly it is mathematically much more interesting to solve the general case with holes. [Quint finally gets his coffee and wanders off, muttering.]

S: Our old equation $w_e = 2n + 6$ has become $w_e = 2c_e + 6$ to account for thin nests. Whence come the 2 and 6? In nice roundish nests, as in Figure 5, most of the exterior cells have two outside walls, but the six corners each have a third wall. Oh! As we go around the nest, we make a net turning of one circle, or 360° . Going from one wall to the next always involves a turn of 60° , one way or the other. When cells are in a row, as in the top row of Figure 5, each interior cell contributes two walls with opposing turns, canceling one another. Exactly six extra walls are needed to turn us around because $6 \times 60 = 360$. Note that even in a convoluted arrangement, as in Figure 6, we get a net of 6 walls or 60° turns. And that explains why we need the mathematical condition of no holes—so only the outside turnings count. Well, Vespa, old friend, our formula

holds for nests with more than one cell but no holes. You can now look for those students to do the drudgery of counting cells.

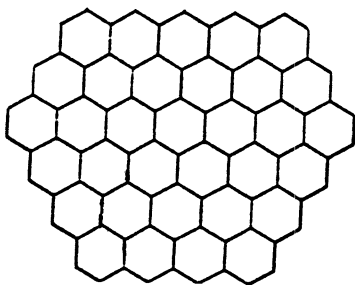


Figure 5.

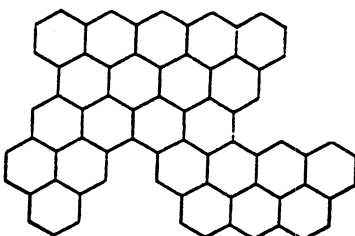


Figure 6.

V: Great! I'm pleased that I can count on your formula, even if I'll have to explain *how* to count. But now that I think of it, your method is a pretty natural way to count the exterior cells.

S: Now that counting is a less daunting task, tell me more about the biology you had mentioned earlier. You noted some advantages of elongated nests.

V: Good evolutionary explanations need a trade off between competing advantages. Then local conditions can push one species to favor one advantage, whereas conditions elsewhere push another species towards a different advantage. Predation by ants in the tropics seems to reward elongated nests. What encourages circular ones? It occurred to me that a circular nest, because of its geometry, might retain heat better than an elongated nest. Both round and elongated nests occur in the Carolinas, where I attempted to measure the temperature in cells of various nests, but the temperature differences appeared negligible. Currently I'm hoping to show circular nests are enough more cost efficient to provide a counterbalancing evolutionary incentive, but until now that required counting the walls.

Q: [Breaking in excitedly] I've solved our problem! We can compute the walls from the cells and exterior cells regardless of the number of holes. Just think of each hole as a small nest without its exterior walls (which are part of the real nest). For a hole of n^* missing cells, the formulas $w = 6n^* - w_i$ and $w = 3n^* + c_e + 3$ give $w_i = 3n^* - c_e - 3$ missing walls. Let m_j be the number of missing cells from the j th hole and c_j the number of these cells that would be exterior were the hole a nest. [See Figure 4.] As usual, n is the number of cells actually in the nest and c_e the number

of cells on the outside. If we filled in the holes, there would be $N = n + \sum m_j$ cells and so there would be $W = 3N + c_e + 3$ walls. Now subtract off the missing walls: $\sum(3n_j - c_j - 3)$. The m_j terms politely cancel. Thus the total number of walls for a nest with h holes is $3n + c_e + 3 + 3h + \sum c_j$. The presence of h is reminiscent of the generalization of Euler's formula $V - E + F = 2 - 2H$ for a polyhedron with H holes. [See [1, p. 68].] You see, there is no need to restrict your theorem to just the special case.

[Remark. The authors are indebted to Lucas Scharenbroich [2] for finding and proving the formula that includes holes.]

S: [After an awkward pause to digest the formula] Well, Quint, thank you. That is amazing, and perhaps such a general formula will come in handy in another setting. I must say that simpler math is usually more helpful to biologists, but not because of their mathematical abilities. Rather, math models necessarily omit many possible biological complications in the hopes of providing clean insight on some facet of a real situation.

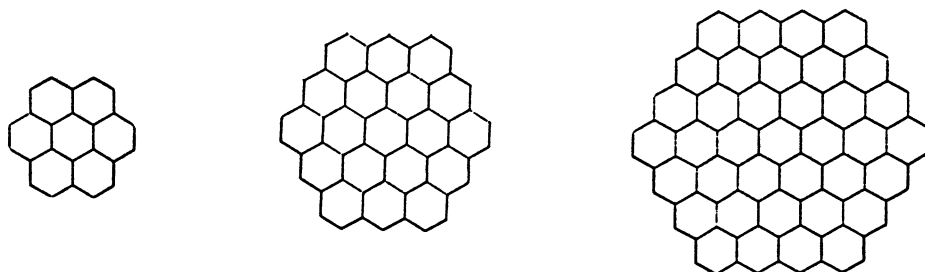
V: Is diplomacy an essential skill to blend mathematical power with biology or is that just your natural personality?

Q: Whether or not my formula is of use, are we done? If the counting formula is all you want, I'll go back to my own amusements.

V: As I mentioned earlier, a formula for the number of walls in the most efficient nest with n cells is needed in order to evaluate actual nests.

Q: So for a given n we need to minimize $w = 3n + c_e + 3$. Clearly, we need to minimize c_e , the other variable.

S: Let's start with the easiest cases—perfectly hexagonal nests have to be the most efficient for their number of cells. [See Figure 7.]



$$k = 1 \quad n = 7 \quad w = 30$$

$$k = 2 \quad n = 19 \quad w = 72$$

$$k = 3 \quad n = 37 \quad w = 132$$

Figure 7.

Q: Actually, we'd need to *prove* these are the most efficient, but that seems more an exercise in mathematical induction than an insightful proof. Instead, let's get some formulas. The number of cells go up by six with each ring around the central cell and that determines the number of cells altogether. That is, the r th ring has $6r$ cells and so for k rings $c_e = 6k$ exterior cells and $n = 1 + \sum_{r=1}^k 6r = 6k(k+1)/2 + 1 = 3k^2 + 3k + 1$ cells. Thus there are $w = 3n + c_e + 3 = 9k^2 + 15k + 6$ walls.

S: While the last formula is correct, we want w in terms of just n . In fact, we want a function $w(n)$ for any n . Let's rewrite $c_e = 6k$ in terms of n .

Q: Convert $n = 3k^2 + 3k + 1$ to $3k^2 + 3k + 1 - n = 0$ and use the quadratic formula to get $k = \frac{-3 \pm \sqrt{12n-3}}{6}$. Because k is positive, use the plus sign. So $c_e = -3 + \sqrt{12n-3}$ and $w(n) = 3n + \sqrt{12n-3}$. Pretty nice!

S: And it makes sense geometrically. The term added to $3n$ is related to the number of exterior walls, which is proportional to the perimeter. The number of cells is proportional to the area and so grows roughly with the square of the perimeter. Conversely the perimeter grows roughly with the square root of the area, which explains why our formula has that lovely square root in it.

Q: There, Vespa, is a simple formula for you.

V: [Quizzically] Maybe, but the number of walls is always a whole number and square roots almost never are. So this formula is clearly wrong almost always.

S: [Drawing nests to find the optimal number of walls] We still need to see if it's close to the optimal number for any n , but it seems like a good candidate to test.

V: But I want an *exact* formula so that I can compute how efficient real nests are.

Q: You must be kidding. I thought biologists wanted simple formulas for insight. Besides, how much error would the approximation introduce into a discipline hardly known for its exactitude?

[Remark. In actuality our class abandoned this project for quite some time in response to our entomologist's insistence on an exact formula. Eventually we came to the following realization.]

S: [after *much* scribbling] Amazing. It looks like our formula is always within one of the exact value and always either low or right on. [See the abbreviated table below.]

n	19	20	21	22	23	24	25
$w(n)$	72	76	79	83	86	89	93
$3n + \sqrt{12n-3}$	72	75.4	78.8	82.2	85.5	88.9	92.2

If we use the ceiling function, which rounds up decimals to the next integer, we do get an exact formula: $w(n) = 3n + \lceil \sqrt{12n-3} \rceil$, assuming that we could somehow prove this formula correct. I have no idea how the ceiling function interacts with square roots.

Q: Finally a mathematically interesting question! I don't know that anyone has toyed with that sort of question since these functions don't appear together much.

S: Let's go back to where the square root appeared: $6k = -3 + \sqrt{12n-3}$ came from $n = 3k^2 + 3k + 1$ for nests with complete outside rings. For a value of n bigger than one of these we start adding new cells. For the first cell we need to build four walls in addition to the two we get from using a notch. [See Figure 8.] The next few cells need only three new walls each since they can take advantage of the just completed cell as well as the adjacent notch.

V: That is exactly how real wasps in temperate climates tend to build their nests! They attach a new cell in any notch on a completed ring and add cells going around until they complete the next ring. Of course, occasionally two wasps start adding cells on different sides of the nest, or other anomalies can arise, such as . . .

Q: [Quickly interrupting] Do they add the cells counter-clockwise, like good mathematicians?

V: I'm not sure that there is much in the literature on that question.

S: Let's see, after the first few cells we add three or four walls to make the most efficient nest. The key is to decide when to add three and when to add four. If we have finished the k th ring, the first added cell needs four walls. There are $k + 1$ cells on a

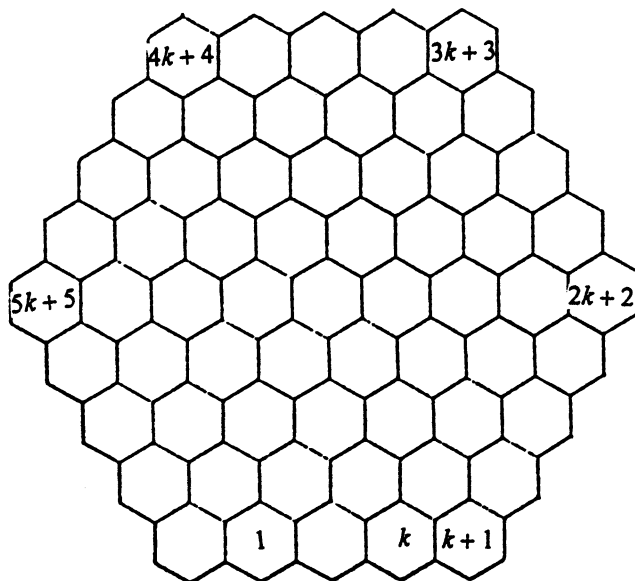


Figure 8.

side in the k th ring, so there are k notches. [See Figure 8.] Hence the second to k th cells need only three more walls. The $k + 1$ st new cell needs four walls, whether it is for a corner cell at the end of the new row or for a middle cell on another side. If we pick an adjoining corner cell, we can add k cells on the adjacent side each with three walls. That postpones as long as possible a cell requiring four walls. Similarly, the four-walled cells are added at the 1st, $k + 1$ st, $2k + 2$ nd, $3k + 3$ rd, $4k + 4$ th and $5k + 5$ th places.

[Vespa falls asleep. A gentle snore provides backdrop to the following algebra.]

Q: When does the square root in $w(n) = 3n + \lceil \sqrt{12n - 3} \rceil$ bump up past the next integer so that the ceiling function increases by one? Let's replace n by $3k^2 + 3k + 1$ plus the number of cells we've added. For $n = 3k^2 + 3k + 1$, of course $12n - 3 = 36k^2 + 36k + 9 = (6k + 3)^2$ is a perfect square. Now $n = 3k^2 + 3k + 1 + 1$ gives $12n - 3 = (6k + 3)^2 + 1$, whose square root will be rounded up to $6k + 4$, corresponding to using four walls to build the first cell in the next ring. Note that $(6k + 4)^2 = 36k^2 + 48k + 16$, so we add only three walls to build succeeding cells until $12n - 3 > 36k^2 + 48k + 16$. Adding up to k cells doesn't force an additional cell with four walls but the $k + 1$ st cell gives $n = 3k^2 + 3k + 1 + k + 1$ or $12n - 3 = 36k^2 + 48k + 21 = (6k + 4)^2 + 5$, so its square root rounds up to $6k + 5$, matching the next time we need four walls to build an additional cell. It is just as routine to show that the remaining jumps occur at the places you specified.

S: How nice—the formula derived from the complete rings easily leads to an exact formula for any number of cells. And the proof is just simple algebra.

Q: Actually, I find our algebraic argument awkward and devoid of insight. Even more, our algebra doesn't prove that the formula gives us the lowest values possible, just that the formula matches the number of walls we get following this building plan. For some values of n it is logically possible that another arrangement could give a smaller number of walls.

S: I see your point. But it is relatively straightforward to check that our arrangements are the most efficient for small numbers.

Q: Let's reconsider the idea of minimizing c_e in order to minimize $w = 3n + c_e + 3$. That is equivalent to maximizing the number of interior cells, for a given n . In effect this shifts the best arrangement for n cells down to the best arrangement of interior cells, a noticeably smaller number. That suggests an induction argument for the proof.

S: I think I will leave such a proof to your prowess, since our formula gives the best one could expect wasps to do and, I am confident, the best possible. [S. nudges V.] Vespa, you can rest assured that our formulas answer your questions completely. How do our formulas compare with some of your actual nests?

V: [Yawning] One of my nearly hexagonal Minnesota nests has $n = 223$ and $c_e = 52$, giving $w = 724$, compared with $w(223) = 721$. Talk about close: an "error" of only $3/721 = 0.4\%$. A tropical nest from my collection has $n = 265$ and $c_e = 98$, giving $w = 896$ and $w(n) = 852$, or an "error" of 5.2% . Evolution certainly can work on such a large difference as the 4.8% between the efficiencies of these nests.

S: I'm pleased with those results, but is the difference any good to the wasps? Or to those studying the wasps?

V: I can't believe you even asked. It's all about efficiency and for natural selection, efficiency is of major importance.

S: So wasps should have evolved to be efficient?

V: Exactly so. And this solution helps us determine how efficient they are.

S: And if they are not being very efficient, should we look for other important factors in their ecology?

V: Precisely! I think you've got it. Only careful observation and possibly experiments can reveal which factors should be included. Your questions and your formulas lead to the next round of research. It is time for me to write some grants so that I can pay students to carry out the fascinating part—collecting real data.

Q: Fascination is in the mind of the beholder. As for me, I'd rather generalize these results. Perhaps there are deeper connections or more elegant proofs. Hmm. What would the corresponding formulas be if the cells were squares or equilateral triangles, the other regular figures that tessellate? I'll bet these same sorts of questions might be more challenging in higher dimensions. There is plenty of material here to occupy a student or even me [or the reader] for a while.

S: I will leave you, Vespa, to your grant writing and you, Quint, to your generalizing. Biology and mathematics as independent disciplines generate their own questions naturally. As an applied area, mathematical biology derives its new questions from biology. So for my part I will seek another colleague in biology for a new problem to whet my curiosity.

Acknowledgments. The authors would like to thank Dr. Jim Poff for whetting our curiosity with the wasp nest problem, guiding our efforts so amiably, and providing the photographs for Figure 1. (The role of Vespa doesn't begin to do him justice.) Also, thanks to Erin Casey and Sean Flannery, the other students in the mathematical biology class, who worked on this problem but graduated too soon to join in the writing of this dialogue. Finally, thanks to Lucas Scharenbroich, a student at the University of Minnesota at Duluth, for finding and proving the formula for the number of walls in nests with holes and allowing us to use it.

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