1999

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Published in *Animal Behaviour*, 1999, **57,** F9–F10.

Submitted 13 October 1998; accepted 17 October 1998.

FORUM

How do they, indeed? A reply to Biegler et al.

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We trained Clark's nutcrackers, *Nucifraga columbiana*, to search halfway between two landmarks while varying the distance between the landmarks (Kamil & Jones 1997). We found that the birds learned the problem readily and generalized to novel interlandmark distances within the range of distances used during training. Unlike some other studies in which responses to proportional distance were obtained (e.g. O'Keefe & Burgess 1996; Tommasi et al. 1997), the nutcrackers showed very precise search and maintained this precision during the transfer test. The distributions of digging locations around the central position were concentrated within ±1–2 cm of the central location for both training and test interlandmark distances (see Figure 2 in Kamil & Jones 1997). We reached two conclusions based on this rather precise transfer: (1) the birds used the relationship between the landmarks (rather than goal–landmark relationships) to solve the problem; and (2) the birds had learned a general principle which they could then apply to new interlandmark distances.

Biegler et al. (1999) propose a model that agrees with our first conclusion but suggests that we were premature in the second. According to their model the nutcrackers learned specific vectors for each interlandmark distance used during training. Then, when faced with a novel interlandmark distance, the birds retrieved the vectors associated with the two interlandmark training distances closest to the novel test distance and averaged the vectors. This would produce search at the halfway point. This process would require use of interlandmark distance, part of the geometric relationship between the landmarks. It would also account for the data we reported without appeal to any general principle of halfway. However, we think there are at least two features of our original data that argue against this model.

First, the Biegler et al. model postulates an additional process during test trials that does not occur during trials with training distances, namely averaging vectors. It seems likely that this additional process would introduce additional error into search behavior on test trials. However, there is no indication of such additional error (see Figure 2 in Kamil & Jones 1997).

Second, we found that the nutcrackers were more accurate locating the line connecting the landmarks than in locating the correct position along that line. This suggests that the nutcrackers were making two separate decisions: one, involving bearings or directional information, to find the line connecting the landmarks and the other, involving distance, to find the correct position along that line. This is inconsistent with the use of vectors (see also Cheng 1994).

However, these inconsistencies do not comprise a crucial test of the model, which should be tested directly. Biegler et al. (1999) suggest two tests. One would be to test nutcrackers with distances outside the range of interlandmark distances with which they were trained, especially at shorter distances. Their model predicts greater error at such short test distances than at the shortest training distance. As part of a larger study exploring geometric rule learning, we have collected data on this point and preliminary (unpublished) analyses do not support the prediction.

Biegler et al. (1999) also suggest that we test the birds with rotated landmarks, varying the distance

between the landmarks during the tests. While the results of such a test would be of interest, they might well be inconclusive. If the birds searched further from landmarks with longer interlandmark distances, this would be strong evidence against the model as Biegler et al. point out. However, if the birds show no such effect, it would provide only weak evidence in favor of the model. Large alterations in the arrangement of the landmarks may cause the birds to respond differently during test trials than during training trials.

However, there are other tests that could be carried out. For example, animals could be trained with a variety of different interlandmark distances, each with its own set of vectors. For some groups, these vectors could have a common principle, such as equal or proportional directional or distance components, while for other groups the vectors could be random with respect to the distance between the landmarks. If the nutcrackers simply learn different vectors for different interlandmark distances, then there should be no differences between such groups. However, if as we suspect, the birds use comparisons among vector components, some groups should learn faster than others. And which groups learn faster may provide important information about the use of geometric principles by animals. We are in basic agreement with Biegler et al. (1999) that further studies are needed before we can answer the question 'How do animals "do" geometry?'

We thank Alan Bond and Reuven Dukas for their comments on the manuscript. Supported by NSF Grant IBN 94-21807.

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