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Virtual Animals

ANTENNAE

The Journal of Nature in Visual Culture

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Antennae (founded in 2006) is the international leading peer reviewed academic journal on the subject of nature in contemporary art. Its format and content are inspired by the concepts of 'knowledge transfer' and 'widenining participation'. On a quarterly basis, the Journal brings academic knowledge within a broader arena, one including practitioners and a readership that may not regularly engage in academic discussion. Ultimately, *Antennae* encourages communication and crossovers of knowledge amongst artists, scientists, environmental activists, curators, and students. In January 2009, the establishment of Antennae's Senior Academic Board, Advisory Board, and Network of Global Contributors has affirmed the journal as an indispensable research tool for the subject, now recommended by leading scholars around the world and searchable through EBSCO.

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Author: Jane O'Sullivan

MINIMAL ANIMAL: SURVEILLANCE, SIMULATION, AND STOCHASTICITY IN WILDLIFE BIOLOGY

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Author: Etienne Benson

The first digital simulations of animal movement were developed in the 1960s by wildlife biologists who wanted to better understand how and why animals moved through their habitats. At the beginning of the decade new methods of electronic surveillance based on lightweight radio transmitters had made it possible to observe in close detail the movements of individual wild animals in their natural habitats over long periods of time (Mitman 1997; Benson 2010). To handle the large amounts of data produced by these techniques, biologists developed computer programs that could automatically plot movements on maps and calculate a variety of statistics. These statistics included the probability of an animal traveling a certain distance in a given time period or turning at a certain angle from its previous direction of movement. The probability distributions could then be used as the basis for simulations. Both the tracking techniques and the simulations they inspired contributed to the imagination of what might be called the "minimal animal": an animal that is nothing but a stochastic pattern traced across a blank page.

The minimal animal was not an invention of the 1960s, but the tracking systems and digital computers that first became available during that period both broadened its reach and changed its character in significant ways. To understand how, it helps to look closely at the material culture and research practices of the era's high-tech wildlife biology. One of the most important sites in this history is the Cedar Creek Natural History Area; a research reserve located about 30 miles north of Minneapolis, Minnesota. It was at Cedar Creek that a statistician and biologist named Donald Siniff wrote some of the first computer programs for analyzing and simulating the movements of animals and where the most elaborate and productive automatic radiotracking system of the time was built (Cochran et al. 1965). The radiotracking system included rotating antenna arrays at the top of two towers, one

100 feet high and the other 70 feet high, along with a number of electrical converters, amplifiers, and filters, thousands of feet of cabling, fifty-two pairs of radio receivers, and several 16mm film cameras, which were used to record the changing signals for later analysis. At any given time the Cedar Creek system could keep track of dozens of free-ranging foxes, rabbits, deer, raccoons, owls, or whatever the biologists had been able to attach radio-tags to.

The Cedar Creek radiotracking system had been designed by Bill Cochran, an electrical engineering whiz hired away from the Illinois Natural History Survey by the biologists in Minnesota after he had built some of the first really effective wildlife radio-tags in the early 1960s. After Cochran moved back to Illinois, one of his assistants, Larry Kuechle, took over the maintenance and improvement of the system. The biologists in charge of the project were Dwain Warner, a Cornell-trained ornithologist with a passion for new technologies, and John Tester, a wildlife biologist interested in radiation ecology and daily activity rhythms. Most of the biologists who used the Cedar Creek radiotracking system had a background in wildlife management and wanted to know more about the movements of animals in order to conserve and manage them more effectively. In 1964, at the urging of a program manager at the Atomic Energy Commission, which was funding much of their work, Tester and Warner hired Siniff as the project's statistician and programmer.[1]

A Sea of Data

One of the major challenges faced by Cedar Creek's biologists and engineers was the flood of data that the radiotracking system could produce. In principle it could determine the location of each tagged animal every 45 seconds. That meant it had the potential to produce 80 "fixes" per hour, 1,920 per day, 13,440 per week, 57,600 per thirty-day month, or 700,800 per year for a single animal. Running at full capacity for a year, tracking 52 two animals simultaneously at 45-second intervals, it could have produced more than 36 million fixes. Physicists had recently become used to these kinds of numbers (Galison 1997, 370-433), but they were new for wildlife biologists. The actual rates of data collection at Cedar Creek never approached these astronomical heights, but they were still much higher than most field studies of animal movements up to that point. Earlier studies of animals' use of space—their migration paths, their home ranges, their territories—had often been based on two data points for each animal. One was the place where it had been tagged; the other was the place where it had been recaptured or killed. Even with the radiotracking system running well below full capacity, it was possible to collect hundreds of locations per animal per day.

Despite its name, the "automatic" radiotracking system was automatic only up to a point. Processing the large number of fixes it was capable of producing in a short time was in fact extremely labor-intensive. The film cameras recorded the signal strength from each of the radio receivers along with the time and the current angle of each of the rotating antennae. Once the film was developed the angle of the maximum signal strength at each time point had to be read off manually, either by Cedar Creek's secretarial staff or by the biologists. The antenna angle at which the maximum signal strength was received gave the direction in which the animal was located; two angles together gave the exact location. Cochran had initially envisioned a semi-automatic system for reading the bearings from film, but he was never able to implement it. Instead they were entered by hand onto data sheets or punch cards along with the time, date and other information. The location of the animal was then triangulated by finding the intersection of the bearings of the two antennae, and the resulting locations were plotted on a map or used for statistical calculations.

In the early days it sometimes took longer to process the data than it had taken for the animal to make the movements. Even once data-processing was routinized it could take six to eight hours to process one day's worth of a single animal's movements. The high labor costs of automatic data collection and the hope that computerization could help reduce those costs were not unique to the Cedar Creek system. In 1965, one advocate of bringing electronic instrumentation into biology explained that a major challenge was "the need to acquire new mathematics and computer techniques to cope with the sea of data which continuous biotelemetering will create" (Slater 1964, 82). Cochran had had little experience with digital computers, however, and the radiotracking system he had designed and built was entirely analog. Each link in the chain transduced the signals it had received from the previous link into a new medium. Only at the end of the chain, when antenna bearings were manually read off the film strips, were the

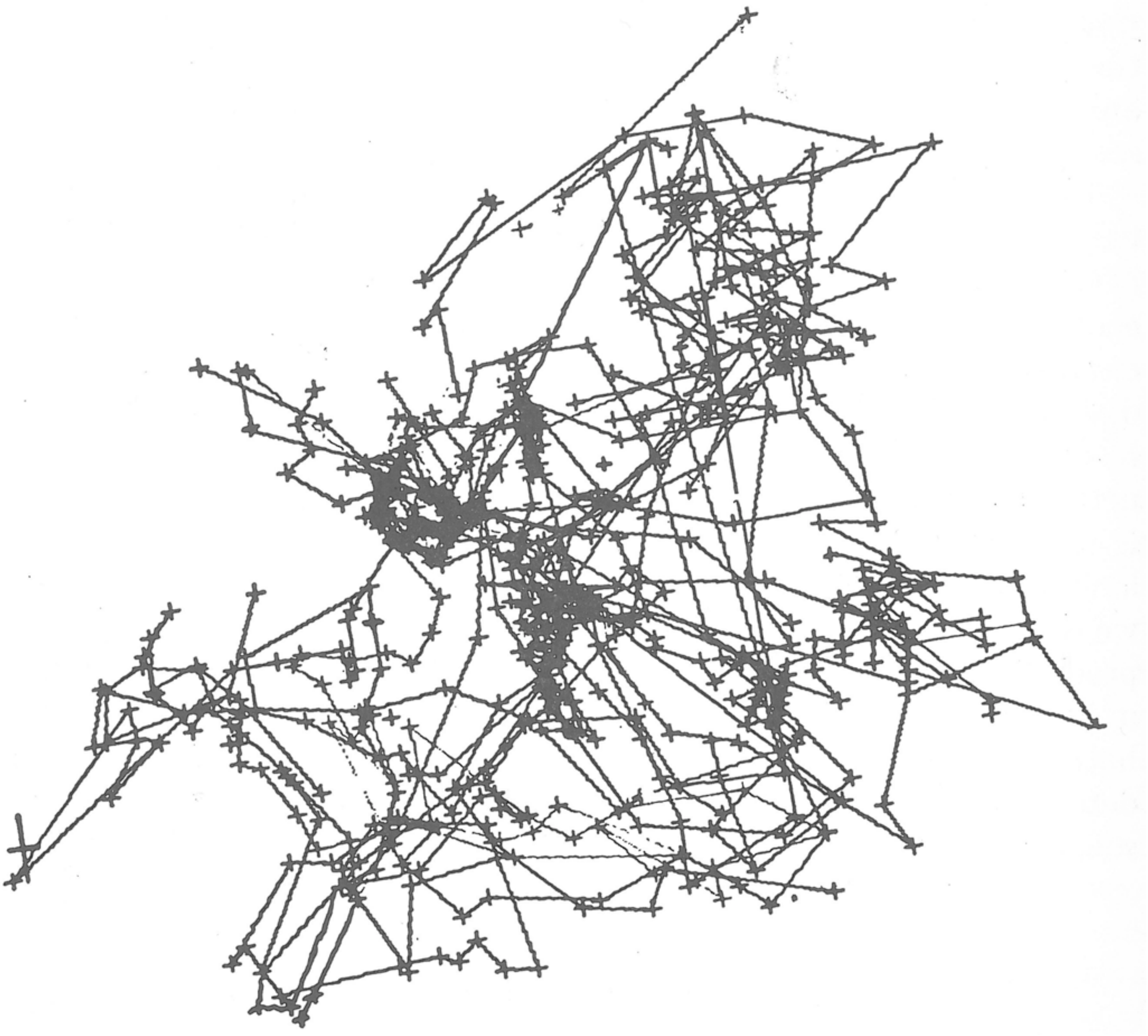


Figure 1: Siniff's FORTRAN programs automated the process of transforming antenna bearings into visual representations of animal movement patterns. (Source: Siniff and Jessen 1969, Figure 1. Reprinted with permission from Elsevier.)

signals recorded as discrete numbers.

One of Siniff's main contributions to the Cedar Creek team was his experience with computer programming, which helped reduce the labor of data processing, even if it could not eliminate it completely. Before coming to Minnesota, Siniff had worked for several years as a biostatistician for the Alaska Department of Fish and Game. In 1962, he had attended a short course on data processing at the University of Washington, where he learned how to write FORTRAN computer programs that could analyze biological data, particularly data about the dynamics of animal populations. When he got back to Juneau, Siniff wrote a leaflet on computers for his Alaskan colleagues. Computers, he explained, could save biologists time by performing multiple regressions and other complex statistical calculations. They could also be used to create hypothetical populations, which would allow biologists to measure the results of different management techniques and environmental factors without having to implement them in the real world. Biologists would still have to use discretion in the interpretation of data, Siniff wrote, but the use of computers "could be one of the most progressive techniques which workers in this field will have at their disposal" (Siniff 1964, 2).

The widespread availability of computers for scientific work was something new in the early 1960s. Short courses such as the one in Seattle taught practical skills and helped inspire quantitatively minded biologists and biostatisticians to use the mainframe computers at their home institutions. They also fostered new connections among people and institutions. One sponsor of the data processing course was the International Business Machine Corporation, a leading supplier of scientific computers and the developer of the FORTRAN language. Another was the Pacific Northwest Computer Research Laboratory, which was affiliated with the Hanford site in Washington State where the United States produced plutonium for its nuclear weapons (Westwick 2003). One of the ecologists working at Hanford was Lee Eberhardt, a mentor of Siniff's. Eberhardt later introduced Siniff to Vincent Schultz of the Atomic Energy Commission, who in turn recommended him to the biologists at Minnesota. The AEC was funding the construction of the automatic radiotracking system at Cedar Creek and wanted to make sure the team included a statistician. The computing and simulation work that took place at Cedar Creek was not comparable in scale or impact to the massive nuclear weapons simulations and physics projects of the era, but it was part of the same network that made those projects possible.

Home Range and FORTRAN

The Cedar Creek radiotracking system provided a unique opportunity to put newly available computer techniques into practice. This was not only because no other system like it existed, but also because Minnesota was a particularly good place for civilian scientific computing in the 1960s. Minneapolis was the home of the Control Data Corporation, which produced the first commercially successful fully-transitorized computer, the CDC 1604, and distributed its own user-friendly version of FORTRAN. The CDC 1604 had been designed by Seymour Cray, who would later build some of the world's fastest supercomputers (MacKenzie and Elzen 1996). Moreover, enthusiasm for using these kinds of new technologies had high-level support at the University of Minnesota in the person of Athelstan Spilhaus, dean of the Institute of Technology and self-described "futurist" (Nierenberg 2000, 347).

After joining the Cedar Creek team in 1964, Siniff wrote FORTRAN programs to analyze the radiotracking data that had been transferred onto machine-readable punch cards (Siniff and Tester 1965, Siniff 1966). Once the cards had been prepared he would take a box or two of them to the University of Minnesota's computer center, where they would be fed into a CDC 1604 along with the control cards that contained his programs. Each data card contained one fix for one animal. The computer could read an arbitrary number of cards, but there was a limit to the total amount of data that could be stored in memory at any one time. The computer allowed the Cedar Creek team to produce maps and calculate statistics much faster than they would have been able to by hand.

Siniff developed his FORTRAN programs in close dialog with the other members of the Cedar Creek team, and with Eberhardt in Washington. A number of different biologists were using the radiotracking system at Cedar Creek, and each of them had his own research questions, but all of them had some interest in how animals used space. Biologists' interest in how individual animals used space had grown since the 1930s. In 1943 the mammalogist W.H. Burt had published a paper distinguishing between home range, which he defined as the area over which an animal usually traveled, and territory, which he defined as the area it defended from other animals. He argued that knowledge of home range was essential for managing wildlife populations. If wildlife managers tried to squeeze a thousand animals into an area where only fifty would fit, they would inevitably fail (Burt 1943, 351). Burt's clear definition of home range and his assertion of its importance inspired other biologists and statisticians to develop a more rigorous understanding of it.

In 1949 another biologist, Don Hayne, wrote an influential paper summarizing different ways of calculating home range sizes. He pointed out that animals used some parts of their home ranges more intensively than others, and he showed how biologists could calculate a "center of activity" from movement data. In the 1950s, building on the work of Burt and Hayne, mammalogists developed the first statistically rigorous models of home range data

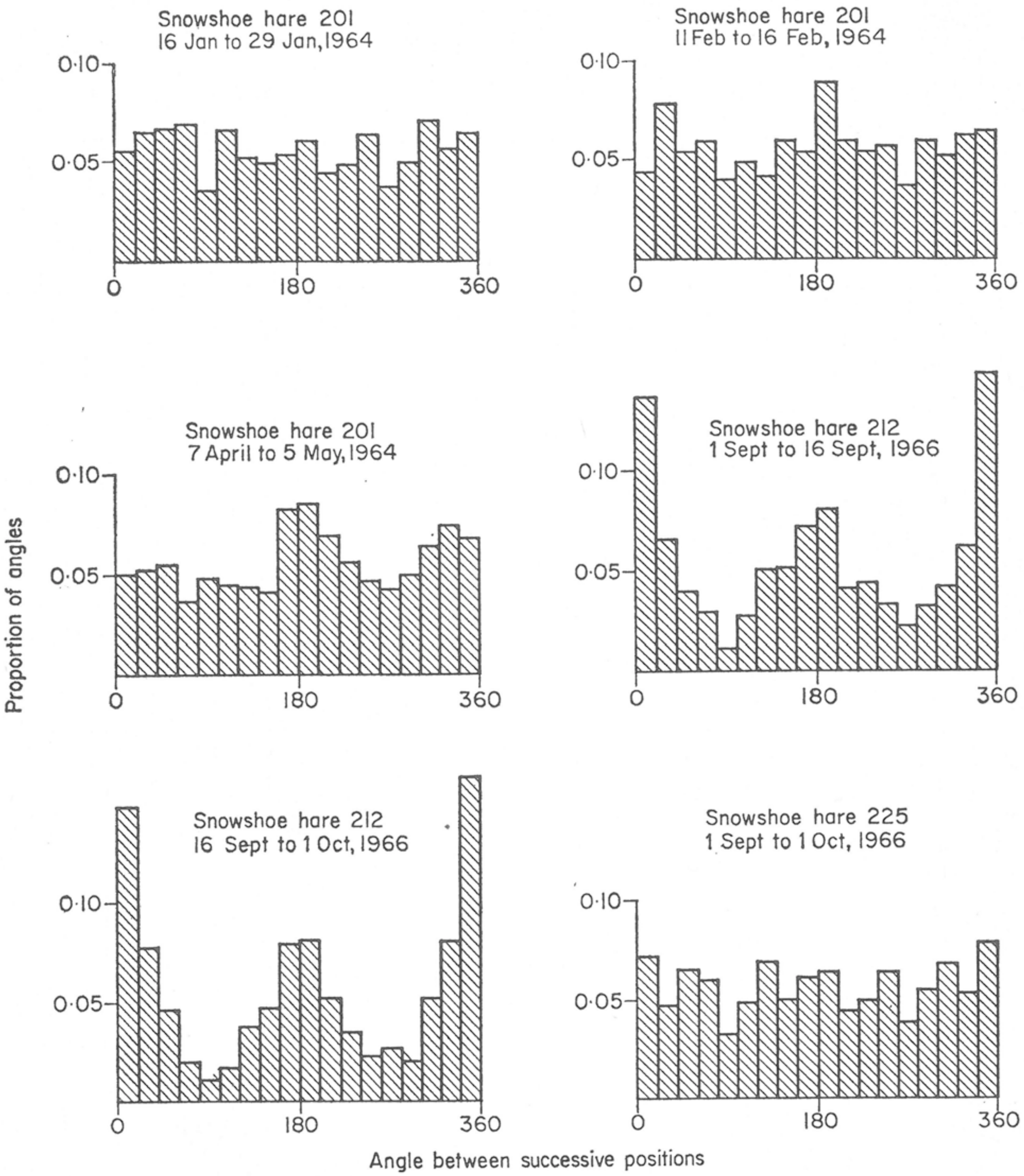


Fig. 5. Some observed distributions of relative angles turned (clockwise) between successive fixes for snowshoe hare.

Figure 2: Statistical distributions of the probabiliy of turning at a particular angle at each step of movement could be extracted from the detailed movement patterns collected by the Cedar Creek system (Source: Siniff and Jessen 1969, Figure 5. Reprinted with permission from Elsevier.)

(Dice and Clark 1953; Calhoun and Casby 1958). For the sake of simplicity the first attempts at modeling assumed that every home range was circular. Most of these models were based on the movements of rodents, which were relatively easy to study. In a typical study the animals were captured, marked, released, and then trapped repeatedly. Each trapping added a data-point to the map of the animal's range.

Radiotracking probably would not have

caught on as quickly as it did without this well-established interest in home range. The technique offered several advantages over earlier methods. Biologists could follow a single animal wherever it went rather than waiting for it to enter a trap placed in a specific location. They did not have to worry that repeated trapping would influence an animal's behavior, and they could collect data much more frequently. In 1966 the biologist Glen Sanderson expressed a sentiment common among wildlife biologists at the time when he wrote that radiotracking was "one of the more exciting recent techniques for studying mammal movements" (Sanderson 1966, 223). Sanderson had been a colleague of Cochran's in Illinois and he and his wife Beverly had used some of Cochran's earliest radio-tags to study the movements of rats near a U.S. military base in Malaya in the early 1960s (Sanderson and Sanderson 1964). Radiotracking also brought new challenges and limitations. As Sanderson pointed out, radiotracking was still expensive and time-consuming and had not yet made many significant contributions to knowledge about animal movements. More data did not lead inevitably to better science.

Perhaps the one area where radiotracking had made a clear contribution was by establishing that earlier models of home ranges as circles or other regular shapes were too simplistic. Animals moved through their environments in complex ways. This was no surprise to most biologists, but radiotracking made it harder to ignore the complexities. In a letter to Siniff written on August 5, 1964, Eberhardt encouraged him to use the data produced by radiotracking to test "the assumptions which have thus far been inaccessible, simply because we largely have been able only to observe endpoints"—that is, because biologists had been limited to gathering a few positions per animal. Eberhardt did not use radiotracking himself, but he and Siniff both thought that the Cedar Creek system provided a good opportunity to advance statistical models of animal movement.

The programs that Siniff wrote converted the antenna bearings to Cartesian coordinates and calculated various statistics, including the distance traveled by the animal, the total area it had traversed, its geometrical center of activity, and its distance at any given time from a reference point or the moments of another animal. He also wrote a program to determine how often an animal turned at particular angles from its previous direction of movement and how often it travelled particular distances in a given amount of time. Another program plotted the coordinates of animal positions on paper. It was clear from looking at these plots and statistics with the Cedar Creek biologists that different species used the landscape in different ways. Siniff was enrolled as a graduate student at the University of Minnesota and had been working at Cedar Creek mostly at nights and on weekends to support his family. By 1966 he had decided that computer simulations might help to explain the differences in movement patterns and could serve as a good topic for his PhD thesis.

Breakdowns and Random Walks

The engineering team at Cedar Creek generally kept the radiotracking system running smoothly, but sometimes heavy winds would damage the mechanisms that rotated the antennae, or there would be a short-circuit or loose connection somewhere in the electronics, or the cameras would stop filming. The biologists would arrive in the morning at the Cedar Creek laboratory building and discover that the animals they had been tracking for days or weeks or months had slipped silently off the map. The engineers would soon get the system up and running again, but the data that had not been recorded could never be recovered. After such breakdowns Siniff remembers kidding the biologists who relied on him to help make maps of their animals' movements: "Don't worry. You want fox data? I'll make you fox data. You want grouse data? I'll make you grouse data." When behavior was coded in digital form, the lines between observation and simulation blurred.

The simulation method that Siniff (1967a) developed for his dissertation was fairly simple. He had already written programs to plot movements on a coordinate system and to characterize those movements statistically. Simulation reversed the process, using the statistical distributions drawn from animal movement patterns to generate new data. First the program randomly generated periods of rest and movement. Then, for each period of movement, the program calculated two numbers. The first indicated how far the animal would move, and the second determined at what angle it would turn. These numbers were selected at each step from probability distributions that were meant to resemble those of radiotracked animals of different species. Instead of using the actual distributions observed by

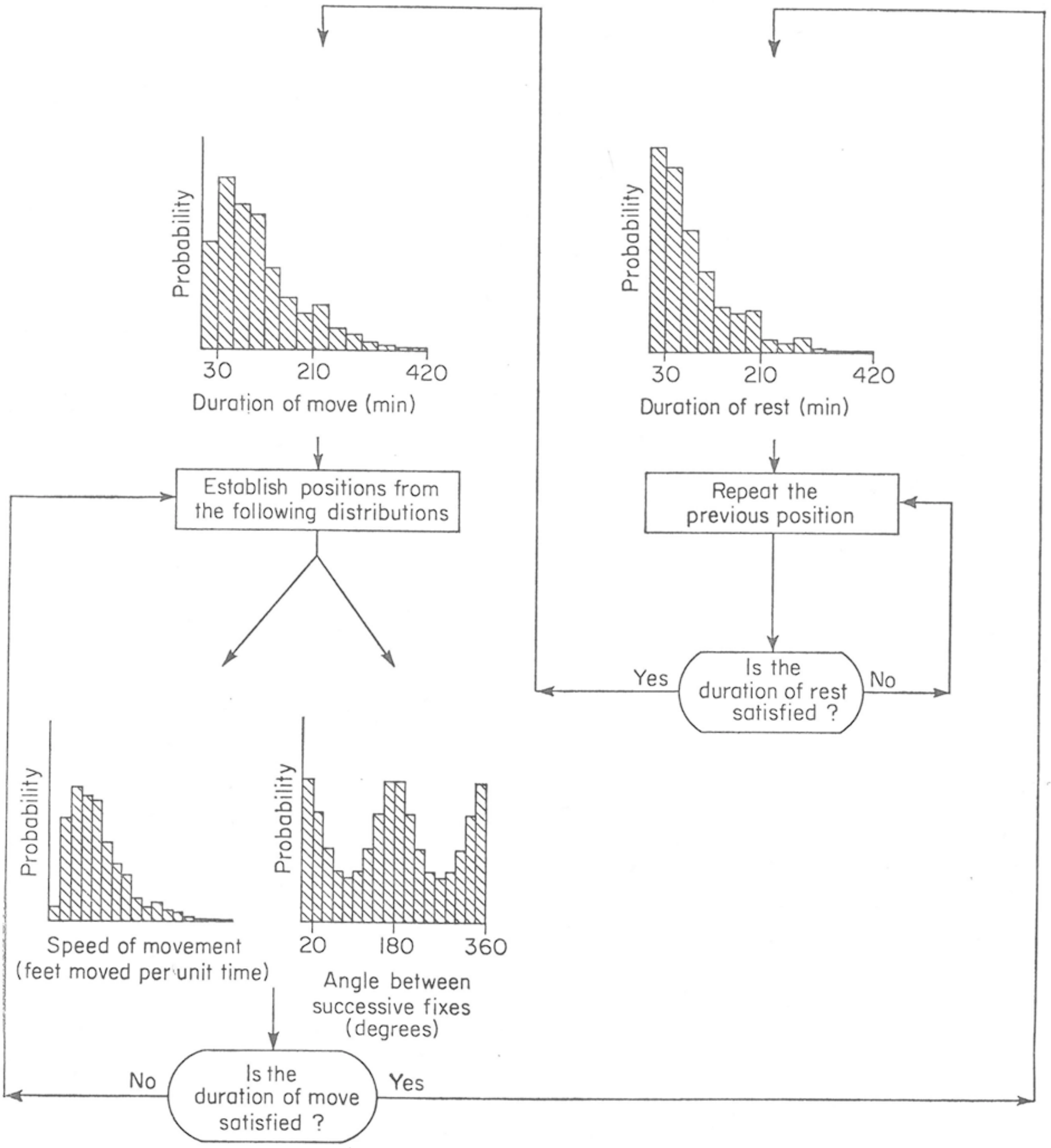


FIG. 10. Block diagram of simulation procedure proposed for animal movement. The distributions used in this figure are hypothetical.

Figure 3: The simulation model that Siniff developed for his doctoral dissertation used simplified versions of the observed statistical distributions to generate new data, which were represented in visually similar ways to empirically observed movements (Source: Siniff and Jessen 1969, Figure 10. Reprinted with permission from Elsevier.)

the Cedar Creek system, the programs used approximations that could be expressed as mathematical equations. Siniff thought that these simplifications would make it easier to understand, in a rigorous way, how the movement patterns of different species varied.

By the time Siniff began using this model it already had a long history in biostatistics. It was a version of the model first described as a "random walk" by Karl Pearson (1905), a major figure in the history of statistics. Pearson had been inspired to think about random walks by the malaria researcher

Ronald Ross, who wanted to know how far a mosquito moving at random would travel in a given amount of time after being released at a particular point (Magnello 2002, 111-112; Klein 1997, 270-274). In the model that Pearson developed, the distance moved with each step was always the same and there was an equal probability of the mosquito turning in all directions. Although Pearson's model was inspired by animal movements, it could be used for any process that changed regularly and randomly over time, whether it was spatial or not.

The version of the random walk used in Siniff's simulation was slightly more complex than Pearson's original random walk in that the probabilities could be adjusted so that some distances and angles were more likely than others. This was important for modeling differences between species. A snowshoe hare nibbling on vegetation might be likely to move short distances in any direction, whereas a red fox searching for prey might be more likely to move long distances forward or backward along a single line.

The British ecologist J.G. Skellam had published a mathematical analysis of random walks in 1951, including the kinds of non-uniform walks used by Siniff. An important difference between Skellam's and Siniff's work was that Skellam was interested in modeling populations, whereas Siniff was interested in modeling individuals. Siniff also had access to a digital computer that could use algorithms to simulate an individual animal's movements, whereas Skellam had focused on developing precise mathematical equations. This was more than just a difference in tools. In the context of microphysics, Peter Galison has distinguished a "platonic" approach that extracts regular underlying patterns from the complexity of observed reality from a "stochastic" approach that builds complex patterns out of many simple, random events (Galison 1997, 743; see also Keller 2003). The focus at Cedar Creek was firmly on the stochastic side of this divide.

The use of computers in ecological research was still new in the 1960s and no one was quite sure what the long-term value of simulation would be (Hagen 2001). Mathematical and statistical techniques had a long tradition in biology, but algorithmic simulation was an unfamiliar and in some ways radical innovation. It had its proponents and its detractors. The ecologist Kenneth Watt, for example, published several books and articles on the promise of systems analysis for ecology in the 1960s (Watt 1966, 1968), in which he argued that computer simulations would make it possible to model and predict the complex interactions found in nature. Watt thought these methods would be crucial in solving challenges of biological resource management. Other ecologists, such as Richard Levins, were skeptical of Watt's claims (Levins 1966, 1968; see Palladino 1991). Levins thought that simulations were good at predicting how a system would behave but bad at generating insights into underlying processes. They could imitate nature but not explain it. Levins preferred mathematical models that, as he put it, sacrificed precision in favor of generality and realism.

Siniff did not directly participate in this debate, but his approach was closer to Watt's than it was to Levins'. He thought that the kinds of mathematical theories advocated by Levins often oversimplified or distorted biological phenomena, whereas simulations could be progressively refined to match observations. In the summer of 1967, after his thesis had been submitted and approved, Siniff published an extract of it as a technical report for the University of Minnesota's natural history museum (Siniff 1967b). The report did not circulate widely, but it nonetheless represented the first published description of the use of a digital computer to simulate the movements of individual animals. The simulation it described had serious limitations, however. One was that it assumed that animals had no memory. The angle and distance calculated at each step were independent of the previous angles and distances. In statistical terms, the random walk was uncorrelated.

This unrealistic assumption helped explain why the results of the simulation did not resemble the data collected by the automatic radiotracking system, no matter how much the probability distributions were adjusted. The longer the simulation was run, the larger the range of the animal became. Given long enough, eventually even a simulated snowshoe hare would have a home range covering all of North America. Another problem was that the simulation assumed that the landscape was completely uniform and that there was no reason for an animal to be in one place rather than another. Even without radiotracking data for comparison, this assumption was clearly unrealistic.

Improving the Fit

Because they can be run and tested relatively easily, simulations lend themselves to iterative development, each new version becoming slightly better than the previous one. With the help of a veterinary researcher named Carl Jessen, Siniff improved the simulation and published the results in an article in *Advances in*

Ecological Research in 1969. The University of Minnesota had upgraded its computers and Siniff and Jessen were able to test their simulations on a CDC 6600, a "supercomputer" that ran up to 20 times as fast as the CDC 1604 (MacKenzie and Elzen 1996, 141).

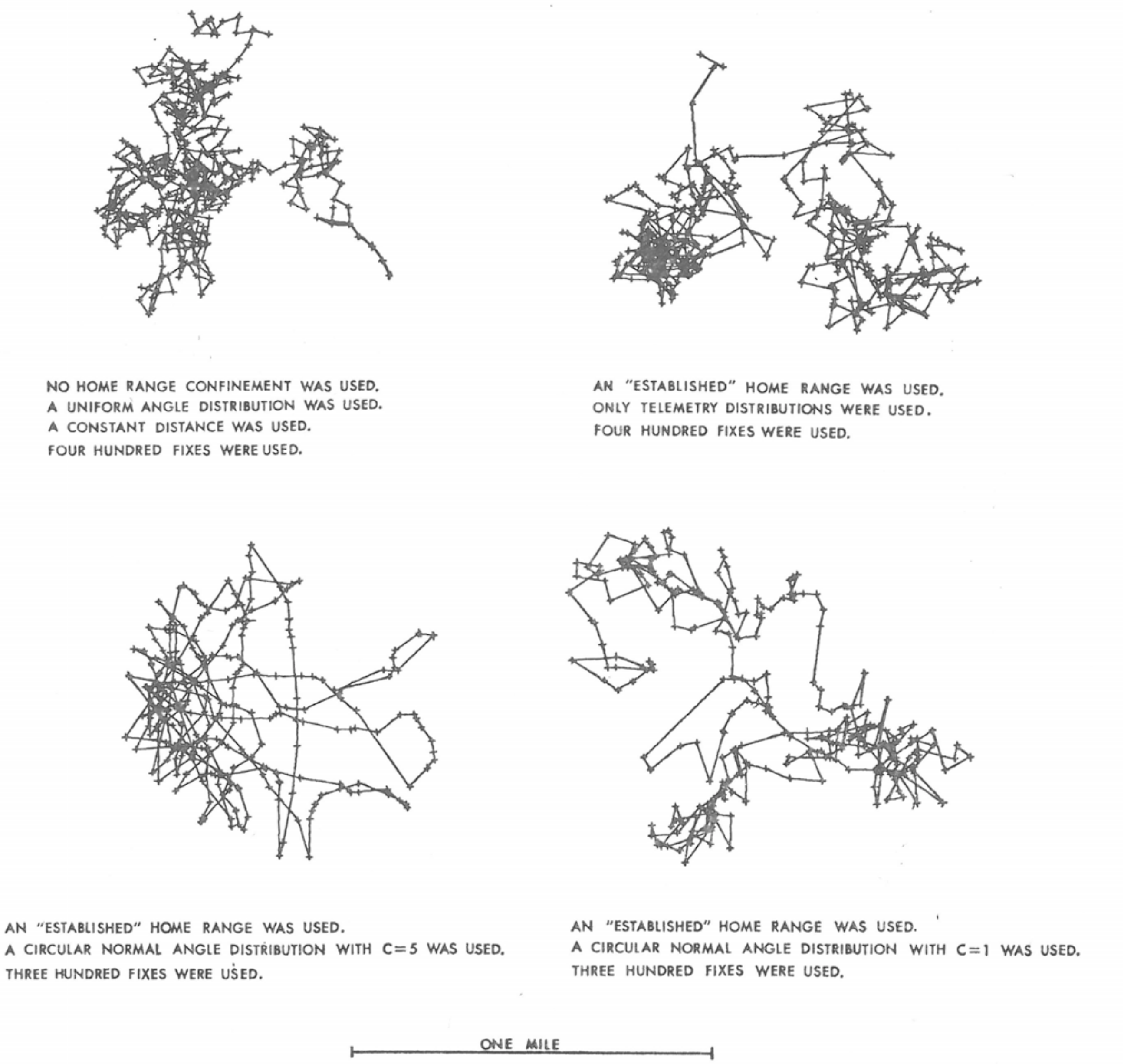
Siniff and Jessen's goal was to generate movement patterns that could not be distinguished from observed telemetry data (Siniff and Jessen 1969, 199). One problem in reaching this goal was knowing when they had reached it. Plotting the movement patterns on paper helped in making qualitative comparisons but not in quantifying the differences. To make these rigorous comparisons Siniff and Jessen identified a statistical measure that could distinguish between movement patterns that were highly clumped and movement patterns that were more evenly distributed across the landscape. This statistical measure showed that Siniff's initial simulation had produced movement patterns that were less clumped than those of real tracking data. Siniff and Jessen assumed that this was because animals liked to spend time in certain areas and not in others.

The new simulation addressed this shortcoming by including a "memory" function that made animals more likely to return to areas they had already visited. This was similar in some ways to another simulation of animal movement that was published in 1969, in which the paleontologists David Raup and Adolf Seilacher modeled the tracks that ancient organisms had left in the fossil record (Raup and Seilacher 1969; see Sepkoski 2012, 223). There is no evidence that these two groups of researchers were aware of each other's work; it is more likely that they drew on similar sources and tools to arrive at comparable results. Siniff and Jessen's new simulation also made it possible to specify the overall shape of the home range in advance, which made it easier to compare different patterns of clumping. The result of these changes was that the simulated data were much closer to the empirically observed movements of animals than when the simulation used an unconstrained,
uncorrelated random walk.

There was no biological reason for increasing the clumping produced by the simulation or for limiting the size and shape of the home range. It was simply a matter of trying to match what had been observed. Siniff and Jessen explained that the "reasons why an animal may decide that an area is desirable or undesirable are not well understood. We only observed that this phenomenon occurred" (Siniff and Jessen 1969, 207). This was the kind of reasoning that Levin had disliked in Watt's work because he thought it focused on surface appearances rather than underlying causes. Siniff and Jessen admitted that their simulation had weaknesses, but they believed it could serve as a structure for incorporating new information: "With the capabilities of large computer systems, we can build such a simulation procedure into as complex a system as our biological knowledge allows" (Siniff and Jessen 1969, 213). Every gap between simulation and observation was an opportunity to learn something knew about how animals made movement decisions.

Despite Siniff and Jessen's optimism that their simulation could be improved even further, this was the last paper that either of them published on simulations of animal movements. Around the time that they were finishing the paper, Siniff was offered a grant by the National Science Foundation to collaborate with the biologist Albert Erickson on a field study of seals in Antarctica. In April of 1968. Siniff wrote to Eberhardt that even though some other seal biologists were opposed to the project, NSF "seems eager to get us deep in the seal business in a hurry." It was an eventful time to be working on marine mammals, with scientists and activists calling for new laws and more research on dolphins, whales, seals, polar bears, sea otters, and other species (Mitman 1999, 157-179; Barrow 2009, 331-336). Siniff jumped at the opportunity offered by NSF and spent most of the rest of his career studying marine mammals, along with a large research project on the feral horses of the U.S. West (Siniff et al. 1986).

Simulations helped biologists offer advice on the likely outcome of different policies, but these simulations were often much closer to the fisheries models that Siniff had learned about in the short course in Seattle in 1962 than they were to the simulations of animal movements that he developed at Cedar Creek. But Siniff's new interest in marine mammals was not the only reason he and the Cedar



NO HOME RANGE CONFINEMENT WAS USED.
A UNIFORM ANGLE DISTRIBUTION WAS USED.
A CONSTANT DISTANCE WAS USED.
FOUR HUNDRED FIXES WERE USED.

AN "ESTABLISHED" HOME RANGE WAS USED.
ONLY TELEMETRY DISTRIBUTIONS WERE USED.
FOUR HUNDRED FIXES WERE USED.

AN "ESTABLISHED" HOME RANGE WAS USED.
A CIRCULAR NORMAL ANGLE DISTRIBUTION WITH C=5 WAS USED.
THREE HUNDRED FIXES WERE USED.

AN "ESTABLISHED" HOME RANGE WAS USED.
A CIRCULAR NORMAL ANGLE DISTRIBUTION WITH C=1 WAS USED.
THREE HUNDRED FIXES WERE USED.

FIG. 14. Fox movement patterns generated with the current simulation model. The upper left movement pattern is the classical random walk.

Figure 4: Siniff and Jessen's improved simulation model made it possible to specify in advance the size of the animal's home range, which made it possible to more closely match observed movement patterns (Source: Siniff and Jessen 1969, Figure 14. Reprinted with permission from Elsevier.)

Creek group turned away from movement simulations and computer programing. There were also practical obstacles. In the early 1970s Siniff helped a graduate student named Gene Montgomery adapt the "Siniff-Jessen model of animal movement" for a simulation study of communication in foxes (Montgomery 1974). However, around the same time a grant request that Siniff had submitted to the University of Minnesota to keep working on movement simulations was denied. Busy with the marine mammalogy work, and unable to hire a programmer to develop the model further, Siniff allowed the simulation work to languish.

He did not completely abandon it, however.

Even without funding, he kept tinkering with some of the movement programs, at one point porting the FORTRAN code over into the newer programming language Visual Basic and digging up the old printouts of fox movements that had been recorded by the Cedar Creek system. Still, he found it difficult to write programs that would calculate home-range-related statistics that other wildlife biologists had come to rely on, such as the minimum convex polygon that included all of the locations where a particular animal had been observed, or the more statistically complex kernel density estimators that gradually became the standard for measuring home ranges over the course of the 1980s and 1990s. Moreover, he had become increasingly skeptical that such simple measures of home range were adequate for understanding animal behavior and ecology in the first place.

Behavioural Minimalism

Although Siniff had moved on and Cedar Creek's heyday as a center for wildlife radiotracking and home range studies was over by the 1980s, scientists elsewhere continued trying to create realistic simulations of animal movement. Computers and radiotracking systems became more powerful, more affordable, and easier to use, and the simulations and the mathematical theories used to understand animal movements became increasingly complex. In 1980, for example, Akira Okubo published a book on diffusion processes in biology. Okubo had started his career as a physical oceanographer before becoming fascinated by the idea of using models of particle diffusion to understand animal swarming and flocking behavior. He saw Siniff and Jessen's 1969 paper as an important attempt to develop simulations on the basis of real data about animal movements. In his view, "the development of telemetry techniques together with the computer has opened a new horizon of research" (Okubo 1980, 4).

More and more wildlife biologists were using the kinds of data analysis and simulation techniques that Siniff and the Cedar Creek team had first developed. The random-walk models of animal movement developed by biologists such as Simon Levin, Peter Kareiva, Peter Turchin, and Paul Moorcroft from the 1980s onwards became increasingly complex (e.g., Moorcroft and Lewis, 2006). Some of these models were so complex that they would have been difficult or impossible to run on the computer equipment available in the 1960s. However, they remained grounded in the idea of the random walk as it had been formulated by Pearson. This was not just a statistical model but also a strategy for research. It started with the assumption that the animal's movements were completely random and then gradually made the model more complex until it matched observations of real animals as closely as possible.

In the mid-1990s the biologists Steven Lima and Patrick Zollner introduced the phrase "behavioral minimalism" to describe this approach to understanding animal movements (Lima and Zollner 1996). Behavioral minimalism can be seen as a specific case of Morgan's Canon, named after the British biologist C. Lloyd Morgan, who argued that "higher" mental capacities should never be used to explain animal behavior when "lower" capacities sufficed (see Radick 2007, 50-83). It should not be particularly surprising that a simulation of animal movement that embodied behavioral minimalism first emerged in the context of the Cedar Creek system. A number of factors converged to make it probable.

One was that the automatic radiotracking system was connected through one of its major sponsors, the Atomic Energy Commission, to other attempts to develop stochastic simulations of complex systems, such as weather or nuclear explosions. Another factor was the nature of the technology itself. Radiotracking produced large amounts of movement data that could be easily quantified, but that did not necessarily have any connection to the environment in which the movements took place. Scientists would sometimes attach additional sensors to radio-tags to gather information about the animal's environment or physiology, but this was atypical. Most commonly, the only data available concerned the animal's location, and the absence of additional information made it hard to explain the animal's movements. This was especially true when an automatic tracking system was used, which freed the biologist from spending long hours in the field.

Very few systems like the one at Cedar Creek were ever built, but automatic tracking became common from the late 1980s onward because of the widespread use of built-in data-loggers and satellite-tracked radio-tags. Once the animals had been tagged, biologists no longer had to immerse themselves in the world the animals encountered. Instead, like the biologists at Cedar Creek, they gathered data remotely, often superimposing movement tracks on maps that were derived from aerial photographs or, later, satellite images (e.g., Varney et al. 1974). These maps could explain some broad aspects of animal movements, but they were usually too static and too simplified to explain any particular animal's movements in detail. Under these conditions, behavioral minimalism was the only option. Ignorance about the causes of observed behavior became randomness in the simulation.

Behavioral minimalism was often a very effective heuristic strategy. In a letter to Eberhardt, written as he was finishing his dissertation in December 1966, Siniff explained that the simplicity of the simulation was an advantage rather than a disadvantage. It was obviously unrealistic with respect to observed tracking data, but it would "enable us to get a better notion of factors influencing the animals' decisions when comparisons are made." Simulation forced biologists to be clear about why they thought a particular animal's behavior was deviating from randomness. Whenever the real animal exceeded the minimal animal, something interesting was happening. In this way Siniff's simulation of animal movements was similar to the simulations of ecosystems or evolutionary processes that other biologists were developing around the same time. As one historian of ecology has argued, the simplifications upon which these simulations were based "could be a powerful stimulant for the scientific imagination, leading to new questions about the real system under study" (Hagen 1992, 134).

The simplifications of behavioral minimalism also carried risks, however. One of these was the risk of implying that animals were just as simple as the simulations used to model them. Researchers in the field of artificial life would later embrace this risk and make it into the philosophical foundation of their field (Helmreich 1998). In the case of animal movement simulations, the risk of mistaking a research strategy for an ontology was often exacerbated by the similarities in the way the movements of real and simulated animals were visually represented. These visual similarities were not accidents but rather conventions that helped establish the realism of the simulations (see Kaiser 2000). In Siniff's work, both simulated and observed animal movements were represented with straight black lines of varying length and orientation, connected at their ends by small black crosses, on a white background. These patterns were labeled with the words "fox" or "snowshoe hare." In the case of the observed data, the landscape and the presence of other animals or events within it had simply been erased, while in the case of the simulated data it had never existed. The similarity between the visual representations helped blur the difference between epistemology and ontology, between the limits to what could be known and assumptions about the kinds of things that existed.

Maps of radiotracking data did not necessarily have to leave out information about the animal's environment. Doing so was a choice that made it easier to see simulated movement patterns as realistic. This is evident in some of the maps and figures that the Cedar Creek group used to present their work. In 1965, the journal *BioScience* published a special issue on biotelemetry that included several papers by the group. One was a study of the response of two radio-tagged deer to a drive census on the Cedar Creek Reserve (Tester and Heezen 1965). The drive consisted of dozens of people moving together across the reserve in order to chase animals out of hiding so that they could be counted. Six of the people participating in the drive carried radio-tags. The paper included illustrations in which the deer's movements and the position of the drive were plotted on maps of Cedar Creek. The maps made it clear that the deer's movement decisions were related to the landscape and to the events taking place in it. The underlying data was still just about movement, but it was movement in context.

These maps were very different from those of another article by the Cedar Creek group in the same issue of *BioScience* (Siniff and Tester 1965). This second article focused on Siniff's data-processing software. The figures in it also showed movement data from real animals, but they omitted vegetation and topography and the presence of other animals or people. They showed only the movements of a single animal on a blank white background. This was the kind of representation that Siniff would later use to show the results of his random-walk simulations. Such representations made the output of the simulations look the same as the results of radiotracking real animals. The omission of the world through which the animal moved rendered the simulation and the plot of empirical data comparable. Simulations that lacked complexity and context could be made to look more realistic by simplifying and decontextulizing representations of data collecting from real animals. This aesthetic leveling also made it easier to slip from the epistemological heuristic of behavioral minimalism to the ontological assumption of the minimal animal.

The Nonminimal Animal

Working as closely as they did with animals and particular landscapes, and with colleagues who had spent many hours in the field, few if any of the biologists at Cedar Creek believed in the ontological reality of the minimal animal that their methods of data collection and simulation suggested. The risk of mistaking strategy for ontology was more real for people who had never studied animals closely than for those who spent their careers observing them. Even though he did not spend as much time in the field as the biologists on the team, Siniff was well aware of how much his simulations left out. This became especially clear, Siniff later recalled, during his conversations with Alan Sargeant, the biologist who had provided the fox data for his models and who used many other methods for understanding animals besides radiotracking (Sargeant 1972). Siniff remembers Sargeant as probably the best field biologist he ever worked with.

One day Sargeant and Siniff were arguing about how well foxes knew their territories. "Oh, Don," Siniff remembers Sargeant saying, "this fox knows every inch of space in its home, in its territory. You cannot do anything out there that it doesn't know about. If I put food out there he knows exactly where it is." Siniff was skeptical, so they agreed to conduct an experiment. They bought a pound of hamburger and threw it into the woods. It was the middle of winter and fresh meat should have been attractive to a fox. Days went by without the radio-tagged fox touching it, so they decided to go out into the field to see what the fox was doing, using the radio tag to locate the animal for visual observation. They saw the fox make a beeline for the hamburger and Siniff thought that Sargeant's faith in the fox's intelligence was about to be disproven. Just before reaching the meat, however, the fox turned and dived through the snow to pull up a garter snake. It knew that the hamburger meat was there but would not risk touching something that had been placed in the woods by the humans who had previously trapped it. At that moment Siniff realized he had underestimated the fox.

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Notes

[1] In addition to published sources, the account that follows is based partly on conversations and email exchanges with Donald Siniff and other members of the Cedar Creek team, particularly William Cochran, Larry Kuechle, L. David Mech, John Tester, and Dwain Warner. I am indebted to them for their generosity in discussing their work. Letters cited are from Siniff's personal papers; copies are in the author's possession. David Sepkoski provided suggestions for situating this story within the history of simulation in ecology and evolutionary biology and Dan Bouk shared his knowledge of the history of statistics. Any errors of fact or interpretation that remain are my own.

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