Filming Fly Eggs: Time-Lapse Cinematography as an Intermedial Practice

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Abstract: This essay investigates time-lapse cinematography as a hybrid, intermedial practice. To interrogate practices of authorship, publication, copying, storage, and especially distribution, it recovers the history of *The Embryonic Development of Drosophila melanogaster*, a film made by Eric Lucey at the University of Edinburgh in 1956. An unusually rich archive makes it possible to recover uses and reuses of time-lapse footage in research, teaching, and other forms of communication.

[Figure 1 here]

The term "intermediality" is used by film and media scholars to evoke the continual dialogue between different forms of mass communication in a larger culture of production and consumption—for instance, the book of the movie or the movie of the book.[1] It is encountered less frequently in histories of science. Yet these too have examined, relationally, how a range of media have shaped the making and communication of knowledge. We have not only histories that focus on one medium (x-ray photographs, microscope slides, laboratory manuals) but also explicitly or implicitly "intermedial" studies, notably of three-dimensional models and of moving images.[2] These have thrown into relief neglected aspects of the flat pages with which most historians are more familiar.

Nineteenth-century embryology is particularly well served by detailed, intermedial histories of wax models. By comparing the production of models and books, these studies have expanded "our view of scientific publication during the great age of print" to include other three-dimensional objects that became indispensable to university teaching. Wax, however, was marginalized by film and other media in the twentieth century.[3] By the mid-1950s, time lapse was generally regarded as "the perfect technique for the observation and recording of the slowly growing embryo." Rather like models, films (of living, developing embryos) became indispensable for teaching and, in some areas, research.[4] Footage was multivalent: practitioners extracted individual frames for analysis and publication in print; and they spliced longer strips into films that also incorporated narration, still images, animated sequences, and other devices for rendering the raw material more intelligible.[5]

Histories of time-lapse methods in embryology have focused on the specificity of film as a temporal medium and on the philosophical implications of digital imaging.[6] This essay takes a different approach. Extending histories that have explored the production and uses of wax models in relation to print and other media, it investigates time-lapse cinematography as a hybrid, intermedial practice.[7] To interrogate practices of authorship, publication, copying, storage, and especially distribution, it recovers the history of *The Embryonic Development of Drosophila melanogaster*, a film made by Eric C. A. Lucey at the University of Edinburgh in 1956 (see Figure 1). An unusually rich archive makes it possible to recover typically obscure uses and reuses of time-lapse footage in research, teaching, and other forms of communication.

THE ERIC LUCEY FILM COLLECTION AND PAPERS

Conrad Hal Waddington, an embryologist best known for the "epigenetic landscape" metaphor (a tool for visualizing developmental pathways), created a Research Film Unit at the Institute of Animal Genetics (IAG) in 1950.[8] Waddington had joined the University of Edinburgh in 1947 and, as director of the IAG, he incorporated film into a research program aimed at unifying genetics and embryology. He had first encountered the application of time lapse to embryology in 1930 at the Strangeways Research Laboratory in Cambridge. There, he had used the "watch glass technique" to cultivate chick and duck embryos *in vitro* and collaborated with Ronald Canti, a pathologist and cinematographer, on a short film based on these experiments.[9] Waddington had been impressed by Canti's films and the capacity of time lapse to reveal otherwise imperceptible cellular dynamics. Twenty years later, he established the film unit and hired Eric Lucey, a recently graduated B.Sc. student with wartime experience in photography, to run it (see Figure 2).[10]

Much like the Strangeways Lab in the 1930s, the IAG film unit was an outlier. Universities in the United States and West Germany increasingly boasted in-house film production facilities, but most British universities could not afford or were indifferent to them. Lucey, an inveterate tinkerer, had only modest resources at his disposal, as he worked mostly on his own in a "large hut" behind the institute.[11] He nevertheless kept filming until he retired in 1989. His favorite camera for time lapse was a Cine-Kodak Special; with it he filmed not only biological phenomena but everything from crystallization to urban traffic. His best-known film, commissioned by the BBC in 1966, used a Fastax high-speed camera to capture the jump of a flea at thousands of frames per second.[12]

After Lucey's death, the University of Edinburgh's Centre for Research Collections inherited his film reels, audiotapes, videocassettes, photographs, and papers and began the process—in collaboration with the Scottish Screen Archive and with funding from the Wellcome Trust—of cataloguing, preserving, digitizing, and publishing the films online. Lucey's daughter, Caroline Marr, donated further material, including letters, vinyl records, and photograph albums, in 2013. Five years later, a selection of Lucey's films was screened with musical accompaniment as part of Timescapes, a series of public events hosted by the Edinburgh International Science Festival—a form of recycling that brought his *oeuvre* to entirely new audiences.[13] In the 1950s Lucey's films were seen by a select few; but a film he completed in 1956, on the embryonic development of the fruit fly *Drosophila melanogaster*, would circulate widely in the 1960s and 1970s.

PUBLISHING ON CELLULOID AND IN PRINT

The *Drosophila* embryo was a marginal experimental object prior to the 1970s. From 1910 to 1940, Thomas Hunt Morgan and his students established the adult fly as a key organism in genetics research. The Morgan school, which moved from Columbia University to Caltech in 1928, became the center of an international network of drosophilists with a shared experimental culture and toolkit that included standardized mutant strains. *Drosophila* reproduced more quickly and prodigiously than other laboratory animals—and all year round. The adult was especially amenable to manipulation, but—in a move that reinforced the separation of embryology from genetics—the fly's tiny, fragile, and opaque eggs were generally excluded from research.[14]

Hermann Muller, a former colleague of Morgan's at Columbia, introduced mutant strains (via the USSR) to the IAG in 1937. Muller returned to the United States in 1940, but the refugee geneticist Charlotte Auerbach maintained his stocks through the war (mutagenizing them with mustard gas) and after.[15] Waddington had first worked with *Drosophila* while visiting Morgan's lab in 1938–1939. As head of the IAG in the 1950s, he diverted surplus fly eggs from Auerbach's stocks for research that compared normal and mutant embryos. Such comparisons were facilitated by the publication of *Biology of Drosophila* (1950), the first book to synthesize information about the fly's embryonic development and adult anatomy. Crucially, the chapter contributed by Yale's Donald F. Poulson used photomicrographs of living, dechorionated eggs to stage normal development in *Drosophila* and, in so doing, prepared the way for experimental work on its developmental genetics.[16]

In the early 1950s Waddington tasked two doctoral students, Sheila Counce and Donald Ede, with investigating the embryos of mutant strains that did not survive into adulthood. He assigned Lucey to their projects, to film abnormal development in the mutant embryos. Equipped as they were with Poulson's photographs of normal stages, the pair did not need Lucey to film normally developing embryos for them. But because it was "impossible to tell whether any particular egg set up for photographing was of a normal or a mutant embryo until development was under way," Lucey ended up filming normally developing embryos too. Ede and Counce analyzed stills from his time-lapse footage in their Ph.D. theses, and Lucey included sequences in *The Embryonic Development of Drosophila melanogaster* (1956), a nineteen-minute, black-and-white sound film that also incorporated narration, diagrams, and (poorly focused) photographs of microscope sections.[17]

Ede and Counce further used Lucey's footage as the basis of a research article in *Wilhelm Roux' Archiv für Entwicklungsmechanik* (1956), a journal of experimental embryology. Time lapse, they argued, facilitated "new observations on those phases of the development which involve large re-arrangements of the embryonic material, in particular on blastoderm formation, gastrulation, and involution of the head." More precisely, they reported aspects of gastrulation that had "not been described elsewhere" but were "well shown" in the film (see Figure 3). They also revised the account of mouth formation that Poulson had advanced in *Biology of Drosophila*. Their claims seem to have been broadly accepted. I have found no evidence of resistance and the article, if not earth shattering, encouraged dozens of similarly cinematographic studies; it would be favorably cited for decades to come.[18]

Lucey received little credit. Ede and Counce thanked him in their 1956 paper, as they might have a lab technician. But they stopped short of including him as a coauthor. Catalogues and lists typically identified the *Drosophila* film not with Lucey but with Ede and

Counce—or just Ede. This was par for the course. With the exception (a decade later) of the "classic" flea-jump paper, on which he appeared as second author, Lucey labored in obscurity.[19]

FILM LIBRARIES AND DISTRIBUTION NETWORKS

Film has been described in this journal as an "infinitely replicable and widely distributable medium that circulates easily across many cultural domains." This may be true today, in the digital era. But copying, distribution, and circulation were not always so effortless. In the recent past, supply was severely constrained by the high cost and material limitations of physical media and by the lack of distributional infrastructure. Even today's sprawling entertainment film industries had first to establish and scale up their own systems for copying, storage, and mass distribution.[20] Laboring on a smaller scale and without the benefit of lucrative commercial markets or promotional apparatus, universities and other institutions "cultivated alternative networks" for niche products. In the United Kingdom, distribution for scientific films was centralized only with the creation of the Higher Education Film Library in 1972.[21]

At first Lucey was the sole distributor of his *Drosophila* film. In a footnote to their 1956 article Ede and Counce explained how to obtain a copy directly from him. From 1959, German university instructors could also rent a copy from the Institute for Scientific Film (IWF) in Göttingen. Lucey's correspondence and other sources indicate that the film circulated widely and was much valued as a teaching aid in the 1960s and 1970s. *Methods in Developmental Biology* (1967), a landmark (U.S.) laboratory manual, endorsed it as a "valuable tool in visualizing dynamic aspects of early development." A review in the (U.K.) *Journal of Biological Education* (1972) recommended it as an "excellent record of insect development suitable for advanced classes." Poulson's copy "suffered" so much wear and tear that he stopped lending it out. Decades of use in teaching left other copies similarly "battered."[22]

All in all, Lucey's film had an extraordinarily good run. As late as 1980 it was still in "constant demand for teaching purposes," in the United Kingdom and overseas. At nearly twenty-five, however, it no longer represented the state of the art in embryology or imaging; the film had become "dated," epistemically and technically. So when Mary Bownes, a young developmental biologist who had recently restaged *Drosophila*, joined Lucey at the University of Edinburgh in 1979, he embarked on a remake with her help. Bownes spent months supplying Lucey with living eggs for filming, but it seems likely that he never completed the project. The original 1956 version remained in circulation well into the 1980s, and Bownes used a silent rough cut in her teaching; supplying her own narration in real time.[23]

Research labs increasingly produced their own time-lapse sequences on (cheaper and more convenient) videotape for private, in-house use in the 1980s. But these were not up to publication standard and so did not circulate widely. In terms of reach, Lucey's *Drosophila* film may not have been superseded until the publication of *A Dozen Eggs* (1991), a collection of embryological time-lapse videos on VHS. Sponsored by the U.S. Society for Developmental Biology as part of an initiative to broaden access to teaching material, *A Dozen Eggs* was distributed by Sinauer, publisher of the leading textbook in the field.[24] It was edited by Rachel Fink, a developmental biologist at Mount Holyoke College who also contributed *Fruit Fly Embryogenesis*, a six-minute video on *Drosophila*. For years Fink had collected, copied, and mailed out tapes of the most teachable time-lapse sequences.[25] *A Dozen Eggs* consolidated her previously informal activities. It would be catalogued, reviewed, purchased by libraries, screened in laboratories around the world, and republished on DVD in 2008—evidence of its enduring relevance into the digital twenty-first century.

Lucey and his *Drosophila* film, meanwhile, faded into obscurity, until preservation, digitization, public exhibition, and online publication (all forms of reuse and recycling) breathed new life into his *oeuvre*.

CONCLUSION

Extending histories of embryological media from print and models to films, this essay has approached time-lapse cinematography as a hybrid, intermedial practice. Doing so has brought into focus significant entanglements between film, photography, and print media (books, theses, journal articles). It has also interrogated practices of authorship and publishing, as well as copying, storage, and distribution—crucial yet neglected infrastructural activities that made viewing possible on a mass scale. As we have seen, the lack of distributional infrastructure significantly limited the reach of scientific film until the creation of specialized library services, such as the IWF, in the second half of the twentieth century. Starting in the 1980s, first videotape and then a succession of digital technologies widened access to production and consumption more than film ever could. Today, moving images are ubiquitous in research, teaching, and other forms of communication. Like models, they should be included alongside print and other media in histories of scientific knowledge.

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Biologists: Natural History Film and the Co-Production of Knowledge in Interwar Britain," *Brit. J. Hist. Sci.*, 2020, online ahead of print, https://doi.org/10.1017/S0007087420000370.

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[10] C. H. Waddington, *New Patterns in Genetics and Development* (New York: Columbia Univ. Press, 1962), pp. 153–154 (impressed by Canti and time lapse); and "Obituary: Eric Lucey, Scientific Film Pioneer," *Scotsman*, 22 Sept. 2010.

[11] Eric Lucey, "Who Can Afford a Film?" in *Film in Higher Education and Research*, ed. Peter D. Groves (Oxford: Pergamon, 1966), pp. 243–275, esp. p. 257. In working largely on his own in a makeshift facility Lucey resembled F. Percy Smith. See Timothy Boon, *Films of Fact: A History of Science in Documentary Films and Television* (London: Wallflower, 2008), pp. 19–22; Gaycken, *Devices of Curiosity* (cit. n. 2), pp. 54–89; and "Obituary."

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[25] Rachel Fink, “A Single Frame: Imaging Live Cells Twenty-Five Years Ago,” *Genesis*, 2011, *49*:484–487, https://doi.org/10.1002/dvg.20736, esp. p. 487.

Figure 1. Screenshot of the unfinished remake of *The Embryonic Development of Drosophila melanogaster* (1956), a film that became an enduring staple of teaching in developmental genetics. Eric Lucey and Mary Bownes, University of Edinburgh, ca. 1980, https://media.ed.ac.uk/media/Drosophila+egg/1_pgc1e9km, CC BY 4.0.

Figure 2. Photograph of Eric Lucey adjusting his apparatus for time-lapse cinematography, ca. 1955. Papers of Eric Lucey, Coll-1484, University of Edinburgh Special Collections, EUA IN1/ACU/A1/5/7.

Figure 3. Grid of sequential photographs showing gastrulation. From D. A. Ede and S. J. Counce, "A Cinematographic Study of the Embryology of *Drosophila melanogaster*," *Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen*, 1956, *148*:402–415, on p. 408. Reproduced with permission of Springer.