

***The Importance of  
Place: A History of  
Genetics in 1930s  
Britain***

**Jennifer Marie**

**University College London**

**PhD Thesis in History and Philosophy  
of Science**

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## Abstract

My thesis develops the concept of ‘settings’ for genetics research in 1930s Britain. It shows that settings were associated with stable ‘types’ of genetics. I establish what these types were and how they remained stable by comparing three characteristics of genetics (funding, research organism, problem choice) at two locations in different settings.

I begin by showing that the Department of Zoology/Biometry (DoZ/B) and the Institute of Animal Genetics (IAG) exemplified locations in two of the three settings for genetics study in 1930s Britain: the academic and breeding settings respectively. I also examine how the settings developed between 1900 and 1940.

My study of funding demonstrates that the DoZ/B had a closer relationship to the Rockefeller Foundation than the IAG. This was mainly due to research quality, because both locations undertook academic activities. Nevertheless, bodies that funded breeding locations, including the IAG, tended to support applied research, while academic locations generally struggled to gain external funding.

My study of research organisms reveals that wild and laboratory organisms were used to gain information about generic organisms at academic locations. At breeding locations domesticated organisms were used to gain information specific to a small group of organisms. I demonstrate that operational behaviour towards organisms also differed between the settings.

Finally, I show that problem choice involved the selection of both organism and research area in the breeding setting, but of just research area in the academic setting. Research areas were more synthetic in the academic setting, with the possible exception of cytogenetics.

These features of genetics formed the ‘types’ associated with the breeding and academic settings. The ‘types’ differed in both content *and* the relationship

between different characteristics. This relationship was a lot closer in the breeding setting than the academic, but provided stability to 'types' in both.

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## List of Abbreviations

### Main Text and Footnotes

ABRD:	Animal Breeding Research Department
ARC:	Agricultural Research Council
DC:	Development Commission
DoB:	Department of Biometry
DoZ:	Department of Zoology
DoZ/B:	Department of Zoology/Biometry
GEB:	General Education Board
IAG:	Institute of Animal Genetics
IEB:	International Education Board
JI:	John Innes Horticultural Institution
MRC:	Medical Research Council
NS:	Natural Sciences Division of the RF
RF:	Rockefeller Foundation
RS:	Royal Society
UCL:	University College London
UoE:	University of Edinburgh

### References

b:	Box
f:	Folder
s:	Series
RG:	Record Group
IAGA:	Institute of Animal Genetics Archives
IEBA:	International Education Board Archives
RFA:	Rockefeller Foundation Archives



## **Chapter One**

### **The Academic and Breeding Settings for British Genetics**

#### **1.1 Introduction**

This dissertation emerges from two main problems with the current historical literature on the history of genetics. The first is that no analytical framework exists to consider the context different research sites provided for genetics investigations. As discussed in section 1.5, Charles Rosenberg has discussed the different context in which genetics research was undertaken in America but there are a number of problems with his work for its application to other countries. As discussed in section 1.9, different research contexts are recognised by historians of genetics but no explicit analysis of the influences on research that existed in these contexts has yet been performed. The second major problem with existing historical literature that this dissertation emerges out of, as discussed in section 1.10, is that beyond a discussion of great intellectual achievements and those that had them there is very little literature on British genetics during the interwar period. This dissertation aims to address these two problems.

#### **1.2 Theses**

Several theses are investigated in this dissertation. My first thesis is that during the 1930s British genetics expanded unevenly across the different 'settings' in which it was studied. More specifically, genetics expanded most rapidly in the medical and breeding settings and, to a lesser extent, in the academic setting. This thesis involves several discrete stages. Firstly, during the 1930s genetics research expanded in Britain. It was studied by a growing number of people and gained new locations for its study. Secondly, genetics was studied in different settings in Britain during the 1930s. Thirdly, genetics grew at different rates in these different settings. Genetics 'locations' in the medical and breeding settings expanded their capacity to support geneticists at a quicker rate proportional to their size than those in the academic setting. More genetics locations were created in the medical and breeding settings but not in the academic setting.

My second thesis is that there was a ‘type’ of genetics associated with each of these settings. Each ‘type’ of genetics was defined by a configuration of ‘defining characteristics’. Thus, my second thesis is that the different settings can be diagnosed by the type of funding bodies they received money from; the types of research organism that were studied there; and the types of genetic problem that were studied there. In this dissertation I focus particularly on the breeding and academic settings.

My third thesis is that ‘characteristics of science’ (i.e. funding, research material, problem choice) interacted with each other and contingencies in ways that gave stability to the types of genetics in the different settings. In this dissertation I investigate how the different defining characteristics of science interacted with each other, and with contingencies, in the context of different locations in the breeding and academic settings.

It should be noted that settings are not seen as causal factors in this dissertation. Instead, they are clusters of locations which had similar types of genetics because they had similar influences affecting them. As such this dissertation will discuss a variety of factors that worked together to cause the effects seen. Some of these, such as funding, were related to the purpose of the location. Others, such as the interests of individuals, were not. However, the latter factors were aligned or misaligned with other causal factors, some of which were related to the location’s purpose. Thus, in thesis three I investigate the interaction of factors that brought stability to the types of genetics found in settings.

### **1.3 Dissertation Structure**

I examine the robustness of my first thesis in Chapter Two. I investigate the history of genetics in Britain between 1900 and 1940, placing particular emphasis on the different settings in which it was conducted. This demonstrates that the medical setting was the most rapidly growing of the settings in 1930s

Britain, and that the academic setting grew least quickly. This was therefore the context in which genetics was researched in 1930s Britain.

I investigate how my second and third theses help one to understand genetics in the British breeding and academic settings in Chapters Two to Five. The principal methodology used is a comparison of the genetics section of the Department of Zoology/Biometry (DoZ/B) at University College London (UCL), with the Institute of Animal Genetics (IAG) at the University of Edinburgh (UoE). In Chapter Two I investigate the histories of these two institutions prior to 1940. This demonstrates that the DoZ/B was located in the academic setting for British genetics, while the IAG was located in the breeding setting for British genetics.

In Chapters Three to Five I compare different characteristics of science (funding, research organisms, and problem choice, respectively) at the DoZ/B, UCL and at the IAG, UoE.

Chapter Three examines funding, especially the influence of the Rockefeller Foundation (RF), on genetics at the two locations. The RF funded geneticists across the British academic/breeding setting divide. By focusing on the Foundation's funding of genetics, similarities and differences between the settings are revealed.

Chapter Four studies research organisms, especially the use of mice for genetics research. Mice were used for research in both academic and breeding locations. This illustrates some similarity in the research organisms used across the settings. However, the mice were used to gain information about different groups of organisms and were treated in quite different ways.

Chapter Five investigates problem choice, focusing specifically on the cytogenetics research conducted at the two locations. Cytogenetics was one of the only research areas to be studied in both the academic and breeding settings. However, deeper investigation of this area revealed that the research topics tackled, and the methodology used, differed between the settings.

Through these studies I investigate the defining characteristics of 1930s genetics in the British academic and breeding settings. These studies also reveal how the defining characteristics interacted to create a stable genetics ‘type’ in the two settings investigated. My comparison of the DoZ/B and the IAG can, of course, only demonstrate that there were differences between the types of genetics at these two locations. To establish whether these differences were representative of those between the academic and breeding settings, I therefore briefly investigate genetics at other locations for its study in 1930s Britain.

## **1.4 Methodology**

My comparison of the type of genetics to occur in the breeding and academic settings is mainly based upon the genetics research performed at the DoZ/B and the IAG. As shown in section 2.5, both locations were representative of their respective settings. They were also both important locations for genetics research during the 1930s, and thus of interest in their own right. The three most important locations for British genetics during the 1930s were the DoZ/B, the IAG, and the JI. This suggested the choice of the DoZ/B as an example of the academic setting. The IAG and the JI were both important sites for genetics and both were located in the breeding setting. Either location could therefore have been used as an example of the breeding setting. The choice of the IAG was made because it was more representative of the setting than the JI. The IAG, unlike the JI, was set up by the Development Commission (DC). This was typical of locations in the breeding setting. The IAG was also recurrently funded by the DC/ARC, while the JI received its recurrent funding from the endowment John Innes left in his Will. The IAG had an agricultural research function, while the JI had a horticultural research function. The former was more common amongst breeding locations.

The medical setting was left out of my analysis because it appeared to be less unified than the breeding and academic settings. Some medical locations were part of universities, such as the Department of Eugenics, UCL and the Social

Biology Department at the London School of Economics. Others, such as the Royal Eastern Counties' Institution and the Burden Mental Research Department were not. Some tended to research eugenics, such as the Department of Eugenics at UCL. Others researched the genetics of disease, such as the Royal Eastern Counties' Institution. This meant that no single location could be representative of the setting. As such, the medical setting appeared to be a research project in itself. Investigating it as part of this project would therefore not have done the subject justice.

## 1.5 Models and Analytical Concepts I: The Concept of Setting

Two main historiographical models guide this dissertation. In this section I introduce the more important of the two: the concept of setting, adapted from Charles Rosenberg's 'contexts' for genetics research.<sup>1</sup> Rosenberg argued that there were:

“three potential contexts in which genetic research might have been expected to develop. These were medicine, plant and animal breeding, and – finally – university departments of biology.”<sup>2</sup>

Each context had a common set of constraints and opportunities which affected how the Mendelian laws were accepted and developed. Or;

“each provided quite different conditions for the pursuit of research based on these new [Mendelian] insights.”<sup>3</sup>

Rosenberg offered no explicit definitions of his three 'contexts' but he described the conditions they provided for research. The breeding context was created by the needs of American agriculture. It provided agricultural experiment stations and a large supply of labour, interested in performing breeding experiments. However, breeding was perceived as a craft, based upon experience. Scientific ideas were therefore not always thought to be necessary. Furthermore, the

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<sup>1</sup> Rosenberg, 1976, 197-207.

<sup>2</sup> Rosenberg, 1976, 197.

<sup>3</sup> Rosenberg, 1976, 197.

research done in this context was directed towards the needs of farmers, not the elucidation of genetics principles. Rosenberg therefore summed up the breeding context:

“By 1900, then, the needs of American agriculture had created an institutionally secure – if, in a sense, intellectually compromising – context for the pursuit of studies in heredity.”<sup>4</sup>

Rosenberg offers little description of the medical context. He stated that the role of physicians was to provide explanations for sickness and to be held up as examples of people who understood disease. This meant that while physicians were ignorant about the causes of disease, they found this hard to admit. Rosenberg stated that the medical profession did not provide institutional support for studying the origins of disease. Support for research in this context was therefore restricted to a few medical schools where there were research facilities.

Due to growth in American universities at the start of the Twentieth Century, there was increasing opportunity to study heredity in the academic context. However, there were few places people could train to become academic geneticists. According to Rosenberg, the role of researchers in the academic context was to publish papers, and this entailed the use of recognised techniques and the linking of research to verified knowledge. Since genetics was not an established discipline at that time, Rosenberg claimed that this encouraged academic geneticists to look towards cytology and embryology for ways to define their problems and for techniques to solve them.

Rosenberg argued that genetics developed very differently in each of these contexts. The breeding context encouraged empirical work on agricultural animals rather than abstract scientific research into the mechanisms of heredity. In the medical context, eugenics came to prominence. Following the excesses of eugenics in the 1920s and 1930s, genetics fell from favour in the medical context. Rosenberg states that it was only around 1955 that genetics research programs in the medical context began to be revived. In the academic context,

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<sup>4</sup> Rosenberg, 1976, 199.

biologists studied the relationship between genetics, cytology and embryology. At Columbia such work led T.H. Morgan and his students to suggest a mechanism for heredity and to unite the methodologies of breeding experiments and cytology.

Rosenberg's concept of 'contexts' is of great relevance to this project. It highlights the important influence places can have on the researches conducted within them. Rosenberg shows that research sites in America provided three very different contexts for genetics research. While Rosenberg's concept is a useful framework, it requires refinement to get the most benefit from it. Rosenberg's descriptions of the locations that the contexts arose from are vague. Due to this, and because he identified potential contexts rather than actual ones, it is not clear whether all the locations for genetics research, or researchers, in 1930s Britain fit properly into Rosenberg's set of contexts. For example, horticultural institutes,<sup>5</sup> animal fanciers,<sup>6</sup> medical research institutes,<sup>7</sup> eugenics institutes/departments,<sup>8</sup> botany departments,<sup>9</sup> zoology departments<sup>10</sup> and independent research institutes<sup>11</sup> do not appear to fit into Rosenberg's schema. Rosenberg's contexts are also descriptions of the kinds of conditions in which genetics research occurred in America. They are not analytical categories that can form the basis for further research into the conditions for research that existed.

To refine Rosenberg's concept so I can investigate the contexts different British genetics locations provided for research, I have classified the locations into three groups, which I call settings.<sup>12</sup> These roughly equate to Rosenberg's three contexts. I then investigate the different defining characteristics of science that

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<sup>5</sup> Such as the JI.

<sup>6</sup> Such as R. Staples-Browne.

<sup>7</sup> Such as the Lister Institute or the Royal Eastern Counties' Institution.

<sup>8</sup> Such as the Department of Eugenics at UCL.

<sup>9</sup> Such as at Manchester University.

<sup>10</sup> Such as that at UCL.

<sup>11</sup> Such as the Strangeways Laboratory at Cambridge, where the director, Honor Fell, collaborated in genetics work with Hans Grüneberg at the end of the 1930s.

<sup>12</sup> Since the word 'context' carries connotations regarding the conditions an institute would provide for the work conducted within it, I have changed the term to setting. A setting is thus a group of locations where genetics research was conducted, which direct their research towards the same goals. Classifying a location in a setting implies nothing about the conditions it provided for research, although I wish to demonstrate in this thesis that locations within a setting provided similar conditions for research. That, however, is my thesis rather than the starting point of my investigation.

existed in the breeding and academic settings to see if there was a type of genetics associated with these settings and, if so, what types.

To classify the locations<sup>13</sup> I have constructed working definitions for each setting:

- **The breeding setting for genetics:** the group of locations in which genetics was investigated, and where the research was intended to aid agriculture, horticulture or animal fancying.
- **The medical setting for genetics:** the group of locations in which genetics was investigated, and where the research was intended to increase understanding of human pathology or human social deprivation and their remedy.
- **The academic setting for genetics:** the group of locations in which genetics was investigated, and where the research was intended to increase understanding of an academic discipline.

There is another important analytical model for classifying locations into settings: hybrid institutions.<sup>14</sup> Barbara Kimmelman has argued that genetics research occurred in America in institutions that were breeding/academic hybrids.<sup>15</sup> Kimmelman defined hybrid institutions as:

“those which manifest, in both administrative structure and functional activity, characteristics of two or more clearly identifiable cultural institutions each with a coherent structure and function. They are therefore not merely institutions with multiple functions or constituencies; if so, virtually every modern institution would qualify. What I refer to as ‘hybrid institutions’ are simultaneously, and quite

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<sup>13</sup> In this dissertation I use genetics location to denote a geographic site where a cohesive group of geneticists, or an individual, performed genetics research. Very often this overlaps with an institution, but not in all cases. For example, the Department of Zoology (DoZ) at UCL represents one location for British genetics between 1933 and 1937 (see chapter two for further details) while the Department of Eugenics at UCL represented another location for British genetics at the same time. Though these two locations for British genetics were in the same institution, I classify them as belonging to separate settings. (The DoZ as a location in the academic setting, and the Department of Eugenics as a location in the medical setting.)

<sup>14</sup> At the 2001 Meeting of the International Society for the History, Philosophy, and Social Studies of Biology, a panel was held on the concept of hybrid institutions. (ISHPSSB, 2001.)

<sup>15</sup> Kimmelman, 2001.



literally, several things in one, and their ‘hybrid’ nature is explicit, purposeful, and manifested in the material form they take.”<sup>16</sup>

This definition of a hybrid institution is useful. I have therefore adapted it for my purposes. I define a hybrid location as one where the research was purposefully intended to fulfil more than one of the objectives which differentiate settings. This means that if there was more than one objective to the research conducted at a location, but there was no definite purpose to this, the location was not a hybrid but one whose setting was under contention. In Chapter Two (section 2.3, especially section 2.3.7) I shall argue that the latter was the case for the IAG towards the end of the 1930s.

## **1.6 Models and Analytical Concepts II: Harwood’s *Styles of Scientific Thought***

In this section I discuss the second model that has been used throughout this dissertation: that provided by Harwood’s *Styles of Scientific Thought*.<sup>17</sup> In his book, Jonathan Harwood identified two conceptions of genetics within Germany, which were associated with geneticists’ attitudes towards culture.<sup>18</sup> Having established which concept different geneticists had, he then identified their institutional workplaces.<sup>19</sup>

To investigate the impact of institutions on their workforces’ concept of genetics, Harwood compared genetics at the Institute of Zoology in Göttingen (Alfred Kühn’s school) and at the Berlin Agricultural College (Erwin Baur’s school).<sup>20</sup> Harwood found that genetics research at the former was mainly conducted on abstract topics, in particular developmental genetics. Genetics at the latter was a mixture of pure and applied research, with transmission genetics the main focus of the pure research. The organisation of the two institutes could only be

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<sup>16</sup> Kimmelman, 2001, 1-2.

<sup>17</sup> Harwood, 1993.

<sup>18</sup> Harwood, 1993, chapter five. Harwood also found that the minority German conception of genetics was the major American conception of it. He attributed this, in part, to differences in the institutional structures of universities in the two countries. (Harwood, 1993, 156-177.)

<sup>19</sup> Harwood, 1993, 195-197.

<sup>20</sup> Harwood, 1993, 197-225.

analysed in detail after the schools had moved to Kaiser-Wilhelm institutes. Despite similar numbers of geneticists, Kühn's school had few departments and was organised by subject matter, while Baur's school had many more departments and was organised by research organism. Kühn's school was less hierarchical than Baur's and more diverse research occurred within each of the departments. However, Baur was on more social terms with his fellow geneticists than Kühn.

Harwood found that the type of geneticist working at the two institutions also differed. Those belonging to Baur's school had vocational careers in mind and agricultural backgrounds. Those of Kühn's school did not generally have technical backgrounds. A difference in their publication outlets was also identified. Kühn's school generally published in academic journals, while Baur's school published in professional breeders' journals, popular newspapers and popular magazines as well as academic journals. The source of funding for the two institutes also varied considerably. Baur's institute received most of its funding from the Ministry for Food and Agriculture and from industry, while Kühn's school received very little money from industrial sources. The final distinction Harwood made between the two schools was the relationship they had with the National Socialist German Workers' Party. Kühn's school was mainly left to its own devices by the Party. Baur's school came under the increasing influence of the Party, despite the strong support the Party found there.

The analysis described above has considerable parallels to my own. Harwood extends his analysis further, however, to argue that geneticists' conceptions of genetics correlated with their attitudes to culture, politics and the specialisation of academia, in a patterned manner. Harwood termed such groups of attitudes 'styles of thought'.<sup>21</sup> He explained the two styles of thought he identified by referring to early Twentieth Century German social history.<sup>22</sup> He concluded his book by arguing that theory choice was also influenced by a geneticist's style of thought.<sup>23</sup>

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<sup>21</sup> Harwood, 1993, chapter seven.

<sup>22</sup> Harwood, 1993, chapter eight.

<sup>23</sup> Harwood, 1993, chapter nine.

Critics of Harwood's thesis point to three major problems. One is that the divide between comprehensives and pragmatics was not as sharp as Harwood seems to suggest.<sup>24</sup> The second is that Harwood did not demonstrate awareness amongst geneticists for the comprehensive / pragmatic division, and thus the ontological status of the categories was not proved.<sup>25</sup> A further criticism has been made of Harwood's methodology because it relies heavily on correlations. As Deichmann pointed out, the lack of geneticist numbers makes the validity of the correlations uncertain.<sup>26</sup>

Harwood's work has been a major influence on this dissertation. Like Harwood, I compare genetics at two locations. However, since establishing styles of thought at an ontological level is methodologically difficult, requiring an enormous amount of research, I have not based my work on the concept of style. Harwood emphasises the backgrounds of geneticists and focuses on the individual, whereas I emphasize the setting of a location and focus on workplace.

### **1.7 Models and Analytical Concepts III: Scientific Funding and the RF**

In Chapter Three I investigate the funding bodies that supported genetics research in Britain. I pay particular attention to the funding provided by the RF. A great deal of scholarship already exists on the RF. The most useful for my work is Robert Kohler's study.<sup>27</sup> Kohler describes the relationship between the RF and the scientists they supported, as one of dialogue. The Foundation collected information from scientists on the state of the field, their individual needs, and their opinions of other scientists. This informed their grant giving such that it was appropriate and gave best value. I have followed such dialogues to make sense of the relationship that existed between the Foundation and geneticists at the DoZ/B, and the RF and the IAG, in Chapter Three (section 3.2).

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<sup>24</sup> Weiss, 1994, 414.

<sup>25</sup> Weiss, 1994, 414. Hopwood, 1994, 245.

<sup>26</sup> Deichmann, 1996a, 87.

<sup>27</sup> Kohler, 1991a.

Kohler has been criticised for over reliance on the RF's documentation, which, Pnina Abir-Am argued, made him reflect the Foundation's perspective rather than assess its impact.<sup>28</sup> Abir-Am has instead focused on the Foundation's policy and how this affected projects that the RF contemplated funding.<sup>29</sup> This approach was also adopted by Lily Kay in her investigation of the Foundation's support for molecular biology at Caltech. She situated the Foundation's interest in molecular biology in its wider social program, arguing that the Foundation was concerned with more than just helping science. Kay argued that the Foundation had enormous influence over the development of molecular biology due to the money it invested and its influence on university appointments.<sup>30</sup> In this dissertation, I adopt the idea that the Foundation tried to encourage certain types of work and certain ways of organising research. In Chapter Three (section 3.2) I establish what types of work the Foundation encouraged at the DoZ/B and the IAG, and how successful it was.

Finn Aaserud<sup>31</sup> found that Niels Bohr adapted his funding proposals and to some extent his institute, to attract Rockefeller funding. Though this is not demonstrated for either the DoZ/B or the IAG, there is a possibility that it occurred at the IAG. Aaserud's work therefore suggests a possible explanation for the direction research at the IAG took.

Aaserud's work is one of many on the Foundation's support of science outside America. Much of this literature argues that the Foundation tried to export American science. Most of the studies focus on the export of American ways of organising science and American priorities for fields of study, though there is also some literature on the export of scientific ideas. For example, Donald Fisher<sup>32</sup> argued that the Rockefeller encouraged the integration of medical schools and universities. He argues that it chose to do so in London because, being the centre of the British Empire, London acted as an example to a large

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<sup>28</sup> Abir-Am, 1982, 343.

<sup>29</sup> Abir-Am, 1982.

<sup>30</sup> Kay, 1993.

<sup>31</sup> Aaserud, 1990.

<sup>32</sup> Fisher (Donald), 1978.

number of countries. Doris Zallen<sup>33</sup> has shown that the Rockefeller funded scientific projects according to its (American) values by favouring interdisciplinary collaborations. Thomas Glick<sup>34</sup> also wrote that the Rockefeller exported genetics into the academic setting in Brazil. Genetics already existed there in the breeding and medical settings. However, the imported genetics became more like the rest of Brazilian science, even as it was transmitted. In this dissertation I consider whether locations that were closer in character to those funded by the Foundation in America were more likely to receive funding.

## 1.8 Models and Analytical Concepts IV: Research Organisms

### 1.8.1 The Right Tool for the Job

In Chapter Four I investigate the research organisms used at different locations in 1930s Britain. This research draws on the historiography of the ‘right tool for the job’. This is the argument that a scientist’s choice of organism depends on the job they want it to do. The ‘rightness’ of an organism is context dependent.<sup>35</sup> Barbara Kimmelman demonstrated this for R.A. Emerson’s use of maize. Emerson argued that maize was the right organism for investigating physiological genetics. Kimmelman showed that Emerson’s choice of maize as a research organism was motivated in part by his position in a breeding location. The place of genetics research in breeding locations was under threat from *Drosophila* genetics, which threatened to make the results gained with commercial organisms irrelevant. Kimmelman claimed that Emerson’s argument was therefore not only for maize but for the importance of work done by geneticists employed at breeding locations.<sup>36</sup> Maize was thus the right tool for keeping geneticists employed in breeding locations as well as for investigating physiological genetics. Bonnie Clause has similarly pointed out that rats were promoted as the right tool for scientific work as a way of promoting the Wistar

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<sup>33</sup> Zallen, 1989.

<sup>34</sup> Glick, 1994.

<sup>35</sup> Clarke (Adele), and Fujimura, 1992a, 4-5.

<sup>36</sup> Kimmelman, 1992.

Institute in Philadelphia which inbred them.<sup>37</sup> In Chapter Four I investigate what organisms were the right tools for which jobs at the DoZ/B and the IAG.

The historiography of the right tool for the job implies that the job comes first although, as discussed above, the job was not always a scientific study. However, authors in a special edition of the *Journal of the History of Biology* showed that this was not always true. While the job sometimes came first,<sup>38</sup> they also found that organisms can create jobs.<sup>39</sup> The right organism is often determined by factors other than scientific work; the work then arises from peculiarities of the organism. Kohler has discussed the importance of *Drosophila*'s utility as a teaching tool to its adoption as a scientific organism.<sup>40</sup> Joan Fujimura has shown the importance of pragmatic factors such as size and reproductive speed for the adoption of mice and rats.<sup>41</sup> Adele Clarke has argued that scientists often use the organism of their teacher or the institute they joined, because this introduced them to networks of access.<sup>42</sup> Organism choice therefore has many dimensions; which of these were important at the DoZ/B and the IAG is investigated in Chapter Four.

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<sup>37</sup> Clause, 1993, 330-331.

<sup>38</sup> Though not from this volume, see for example, Kohler, 1991b.

<sup>39</sup> Lederman and Burian, 1993. In this volume see for example Burian, 1993.

<sup>40</sup> Kohler, 1994, 33-37.

<sup>41</sup> Fujimura, 1996, 7.

<sup>42</sup> Clarke, (Adele), 1987, 326, 340.

## 1.8.2 Model Organisms

In Chapter Four I investigate differences between the information gained from research organisms. One concept which is highly relevant to this is the idea of a model organism. Angela Creager has pointed out that the term ‘model organism’ properly has two aspects to it. Firstly, model organisms are used to investigate general biological questions which apply to organisms beyond themselves, such as how genes are transmitted between generations or why cancer cells multiply rapidly. The second aspect of model organisms Creager identified was their function as a representation of how other organisms can be used to investigate similar questions.<sup>43</sup>

In the history of genetics, model organisms have mainly been studied with regard to the first aspect Creager identified. For example, Kohler has discussed how *Drosophila* were constructed into model organisms to investigate how genes are transmitted between generations.<sup>44</sup> Cheryl Logan has looked at the historical process by which it became acceptable to use one species as a model organism through the case of the Wistar Rat.<sup>45</sup> In Chapter Four I investigate whether different organisms were used as model organisms in this respect at the two locations.

## 1.9 Literature Review I: Past Work on the Breeding and Academic Settings for Genetics

My dissertation adds to historians understanding of the settings in which genetics research was conducted, regardless of whether it was conducted in Britain or not. In this section I discuss the literature that already exists on the breeding and academic settings, and how my work will add to the understanding of settings that already exists.

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<sup>43</sup> Creager, 2002, 4-5.

<sup>44</sup> Kohler, 1994, 87-89.

<sup>45</sup> Logan, 2001.

### 1.9.1 Literature on the Breeding Setting

Research on genetics in the breeding setting has mainly focused on America. In her thesis Kimmelman argued that until 1915 genetics was an agricultural discipline in the United States.<sup>46</sup> Her argument is supported by Jan Sapp who agreed that there was little difference between genetics and breeding in the United States before 1915.<sup>47</sup>

The presence of a breeding setting for British genetics has been noted by a number of authors. Daniel Kevles has discussed how agricultural experiment stations conducted genetics research in America, and compared this to the British situation where many of the geneticists were breeders or horticulturalists.<sup>48</sup> Robert Olby's work on the establishment of the John Innes Horticultural Institution (JI)<sup>49</sup> and the Edinburgh Animal Breeding Research Department (ABRD)<sup>50</sup> reinforces Kevles suggestion that British geneticists worked mainly in breeding locations during the early part of the Twentieth Century. Paolo Palladino has also discussed the work of Rowland Biffen in the Plant Breeding Institute, Cambridge,<sup>51</sup> and compared the genetics research of three breeding institutes throughout their histories.<sup>52</sup>

The works of these authors are more suggestive regarding the extent of the breeding setting than conclusive. Olby's studies both focus exclusively on one institute, while Kevles acknowledges that his work is a review of the literature as it stood in 1980 with speculations based upon it.<sup>53</sup> Palladino's work is also limited to three institutions.

It is difficult to compare the extent of research in the breeding setting with that in other settings from this work. Olby and Palladino only discuss the breeding

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<sup>46</sup> Kimmelman, 1987, 3.

<sup>47</sup> Sapp, 1983, 336.

<sup>48</sup> Kevles, 1980, 451-453.

<sup>49</sup> Olby, 1989.

<sup>50</sup> Olby, 1991a.

<sup>51</sup> Palladino, 2002, chapter three.

<sup>52</sup> Palladino, 2002, chapter two.

<sup>53</sup> Kevles, 1980, 441-442.



setting;<sup>54</sup> while Kevles's and Olby's work only studies the period prior to 1930. With the death of William Bateson in 1926 there is good reason to suppose that the relative importance of different genetics settings in Britain had changed by the 1930s. By providing a survey of genetics in Britain I establish the extent to which genetics was conducted in the various settings in 1930s Britain.

A more important gap in the work of Kevles and Olby is that they do not discuss the context the breeding setting provided for genetics research in Britain. Olby's studies focus on the politics surrounding the establishment of two breeding locations for genetics, while Kevles concludes:

“Perhaps genetics in Britain was also affected by the fact that there ... a large proportion of the people working in the discipline [of genetics] seem to have been breeders and horticulturalists.”<sup>55</sup>

Kevles cannot therefore conclusively state that the breeding setting affected the work of geneticists, and can far less conclude what sort of effects it might have had. Palladino's work looks at the major types of work done at three Plant Breeding Institutes but is not an in depth study of any of them.<sup>56</sup> Neither does he consider all the types of breeding locations that existed in 1930s Britain. Animal breeding and horticultural institutes are not discussed. My focus on an animal breeding institute therefore fills an important gap in the literature; first because of the type of breeding institute I study and second because I study the institute in depth.

### **1.9.2 Literature on the Academic Setting**

The majority of work on the history of genetics has focused on the discipline within an academic setting. The Morgan group,<sup>57</sup> George Beadle (later in his

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<sup>54</sup> Palladino does discuss the medical setting later in his work, but does not directly compare it to the breeding setting.

<sup>55</sup> Kevles, 1980, 453.

<sup>56</sup> Palladino, 2002, chapters two and three.

<sup>57</sup> See for example, Kohler, 1994, Kay, 1993 and Carlson, 1974. See Allen, 1978, Lederman, 1989 and Shine, 1976 for Morgan. See Adams, 1994 for Theodosius Dobzhansky.

career)<sup>58</sup> and J.B.S. Haldane<sup>59</sup> all worked in the academic setting. Bateson also worked at Cambridge University until 1910, which is when historians of science tend to lose interest in his work.<sup>60</sup> Of the geneticists who did not work at universities, many of those studied in the history of science worked at locations in the academic setting, as it is defined above. This applies, for example, to Richard Goldschmidt (when he was in Germany),<sup>61</sup> Alfred Kühn<sup>62</sup> and Boris Ephrussi.<sup>63</sup>

While much of the history of genetics is the history of academic genetics, the academic setting has not been explicitly investigated. It is therefore not possible to tell what restrictions the setting placed on work and what opportunities it afforded. The fact that so many of the geneticists written into the history of science were academic geneticists suggests that the setting was conducive to genetics research, but no studies have been done to investigate the reason for this. My dissertation will investigate the academic setting in detail. In doing so it will add to the understanding historians of genetics have of the working context shared by many of the geneticists we know about.

### **1.9.3 Comparisons of the Breeding and Academic Settings**

The only comparisons that have been made of the breeding and academic settings for genetics are Rosenberg's study, discussed in section 1.5, and Harwood's, discussed in section 1.6. Rosenberg based his work entirely on the American situation, while the breeding and academic locations Harwood compared were in Germany. No such comparison has been done for Britain.<sup>64</sup> My work will therefore add an analysis of genetics settings in Britain.

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<sup>58</sup> See for example, Kay, 1989, Kohler, 1991b and Dronamraju, 1991.

<sup>59</sup> See for example, Sarkar, 1992, Dronamraju, 1993, Adams, 2000, Shapiro, 1993 and Mayr, 1992.

<sup>60</sup> See for example, Coleman, 1970, MacKenzie, 1981, Olby, 1987, Darden, 1977 and Farrall, 1975.

<sup>61</sup> See for example, Allen, 1974, Dietrich, 1995, Piternick, 1980, Richmond, 1987 and Gilbert, 1988.

<sup>62</sup> See for example, Rheinberger, 2000, Harwood, 1985 and Egelhaaf, 1996.

<sup>63</sup> See for example, Burian, Gayon and Zallen, 1991 and Kohler, 1991b.

<sup>64</sup> For a discussion of the state of the literature on British genetics in general, see section 1.10.

Rosenberg and Harwood's comparisons of the academic and breeding settings are quite different. Rosenberg focuses on the circumstances the two settings provided for scientific work. Harwood does not explicitly compare the two settings, just two locations which can be categorised as breeding and academic. It is therefore not possible to tell whether differences between the locations he studied were representative of differences that existed between the breeding and academic genetics settings in Germany. Whether the differences Rosenberg identified are applicable outside America is therefore currently not known. My work will help to indicate this.

## **1.10 Literature Review II: Past Work on the History of British Genetics**

One of the intentions of my work is to synthesize and expand our understanding of genetics in early Twentieth Century Britain. In this section I show that the history of British genetics has been little studied for the interwar period. Those studies that have been done tend to focus on individuals and specific intellectual achievements. This makes it very difficult to obtain any coherent picture of what genetics was like in Britain during the interwar period. The work on British genetics that exists has not been integrated, but even when it is taken together, the picture that emerges is a partial one of intellectual achievements and great scientists. What genetics research meant, and what it was like, for most practicing geneticists is not possible to discern from the literature.

In 1993 Harwood claimed that the history of genetics, as written to that date, had more or less been the history of British and American genetics.<sup>65</sup> Newer works, such as Harwood's own, have added to our understanding of genetics in Germany, France, Russia and Spain,<sup>66</sup> but in the main Harwood's criticism still holds true. However, this does not mean that the history of genetics in these two countries is complete. As Kimmelman pointed out in 1987 the history of

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<sup>65</sup> Harwood, 1993, 4-5.

<sup>66</sup> See for example, Harwood, 1993, Burian, Gayon and Zallen, 1988, Adams, 1968 and Pinar, 2002.

American genetics tends to begin between 1910 and 1915.<sup>67</sup> This is also the time when the history of British genetics becomes less well defined, as discussed below.

Between 1900 and 1910 the history of genetics in Britain has been comprehensively examined. Work has been done on the Cambridge geneticist, William Bateson,<sup>68</sup> the controversy he had with the biometricians,<sup>69</sup> and the people who worked alongside him at Cambridge.<sup>70</sup> Work has also been done on the contributions of G.H. Hardy to population genetics,<sup>71</sup> A. Garrod to human genetics<sup>72</sup> and R. Biffen to the genetics of plant breeding.<sup>73</sup>

Some works look at Bateson in the period following his move to the JI in 1910.<sup>74</sup> These tend to focus on his response to the chromosome theory.<sup>75</sup> The period after 1910 also benefits from Daniel Kevles's<sup>76</sup> and Stephen Brush's<sup>77</sup> investigations into the acceptance of the chromosome theory in Britain. However, following Bateson's move to the JI, the history of genetics in Britain becomes rather hazy. What is well studied is the work of a number of key geneticists. Thus the population genetics of J.B.S. Haldane and R.A. Fisher have a well established place in the literature.<sup>78</sup> Haldane, Fisher and Lionel Penrose's work on human genetics during the 1930s is also part of the established literature.<sup>79</sup> The work of

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<sup>67</sup> Kimmelman, 1987, 2.

<sup>68</sup> See for example, Coleman, 1970, Olby, 1987, Darden, 1977, Harvey, 1995, Dunn, 1965, chapter six, Sturtevant, 1965, 29-32, Carlson, 1966, 13-16, 49-51.

<sup>69</sup> See for example, MacKenzie, 1979, MacKenzie, 1981, Farrall, 1975, Dunn, 1965, 116-117, Carlson, 1966, 9-13, Bowler, 1989, 116-122 and Provine, 1971, chapters two and three.

<sup>70</sup> See for example, Ankeny, 2000, Richmond, 2001, Dunn, 1965, 82, Sturtevant, 1965, 30, 134-135.

<sup>71</sup> See for example, Dunn, 1965, 84, 122, Provine, 1971, 133-134 and Crow (J.F.), 1999.

<sup>72</sup> See for example, Sturtevant, 1965, 100, 126, Dunn, 1965, 67-68, 83-84 and Carlson, 1966, 166-167.

<sup>73</sup> See for example, Palladino, 2002, chapters two and three and Dunn, 1965, 124-125.

<sup>74</sup> Olby, 1989 looks at Bateson's move to the JI and the foundation of the institution.

<sup>75</sup> See for example Cock, 1983. This is also discussed in Olby, 1989, 507-508.

<sup>76</sup> Kevles, 1980.

<sup>77</sup> Brush, 2002.

<sup>78</sup> Sarkar, 1992, Provine, 1992, Provine, 1971, chapter five, Maynard Smith, 1992, Bowler, 1989, 140-141, Dunn, 1965, 197-201 and Sturtevant, 1965, 108-109.

<sup>79</sup> Kevles, 1985, Smith (M.), 1999, Bodmer, 1992, Dunn, 1965, 173 and Schneider, 1996, 300-301.

E.B. Ford,<sup>80</sup> Conrad Hal Waddington and Cyril Darlington has also been discussed by historians.<sup>81</sup>

As well as work on such key figures as those described above, some general histories of genetics mention less well known figures. L.C. Dunn, for example, very briefly mentions that H. Onslow, M. Wheldale, Rose Scott-Moncrieff and others worked on the pigmentation of flower colours during the 1920s and 30s.<sup>82</sup> A.H. Sturtevant mentions F.A.E. Crew's and Rowena Lamy's 1935 explanation for why certain mutations were autosomal in one species of *Drosophila* and sex linked in a closely related species, and its confirmation a year later by H.P. Donald.<sup>83</sup> Sturtevant also mentions D.G. Catcheside's 1939 discovery that position effect can be reversed in the next generation in *Oenothera*; Charlotte Auerbach's and J.M. Robson's discovery in 1941 that chemicals can cause mutations;<sup>84</sup> and Guido Pontecorvo's linkage studies in *Aspergillus* during the 1940s.<sup>85</sup> Mark Adams also mentions that population geneticists at UCL repeated the work of Russian geneticists in the 1930s.<sup>86</sup>

One of the major gaps in the history of British genetics from 1910 to the 1940s is the lack of any comprehensive survey of what genetics research was occurring and who was studying it. The works described above fall into two categories, they are either works about a key individual, or they are part of a general intellectual history of genetics. None of the works can therefore provide any sense of how much genetics research was occurring in Britain, or what it was being done on. Without this it is impossible to tell whether the work done by British geneticists that is written into the history of genetics is representative of work done at the time. By providing a general history of British genetics in Chapter Two (section 2.4) I fill this gap in the literature and I provide a

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<sup>80</sup> Zallen, 1999 and Hooper, 2002.

<sup>81</sup> For Waddington see Lewin, 1998, Gilbert, 1991 and Yoxen, 1985. For Darlington see Harman, 2001, Sturtevant, 1965, 78. Sapp, 1987, 166-7, 169 discusses both men from the 1940s onwards, and Carlson, 1966, 178 discusses Darlington's 1944 plasmagene theory.

<sup>82</sup> Dunn, 1965, 176-177. Carlson, 1966, 167 also mentions Wheldale's work on flower pigmentation.

<sup>83</sup> Sturtevant, 1965, 114. Crew and Lamy's work is discussed in chapter six.

<sup>84</sup> Sturtevant, 1965, 72.

<sup>85</sup> Sturtevant, 1965, 56. Pontecorvo's work is discussed in detail in Carlson, 1966, 188-195.

<sup>86</sup> Adams, 1968.

framework by which the works described above can be integrated to form a history of British genetics.

Another major gap in the literature is that very few works on British genetics discuss where the work was done or the context the location provided for research. Two exceptions are Paolo Palladino and Robert Olby's work. Palladino studied plant breeding in Britain from the 1910s onwards. He discusses the extent to which the three British Plant Breeding Institutes provided a context for genetics research, arguing that not all plant breeders thought Mendelian genetics was important to their work.<sup>87</sup> Palladino also studied the controversy over the use of inbred mice for cancer research, and the genetics work done at St. Mark's hospital.<sup>88</sup> Palladino does not provide the sort of analysis I described above however. His work focuses on the extent to which genetics was studied in the plant breeding field, but it does not indicate what proportion of genetics studies occurred there. Furthermore, Palladino does not look at animal breeding locations, such as the Edinburgh IAG, or horticultural breeding locations, such as the JI. It is therefore not possible to know whether similar studies were conducted at these locations to those studied at the Plant Breeding Institutes. In terms of the medical setting, Palladino's work provides some examples of work that occurred, but again there is no indication of how representative they were, or the extent to which this setting supported genetics research. Robert Olby has also briefly studied the foundation of the ABRD at Edinburgh (later the IAG) as part of his research on state support of agricultural research.<sup>89</sup> Olby's work indicates that genetics work occurred in a breeding context at Edinburgh, but because he only studied the foundation of the institute he gave no indication of the type of work that occurred there.

Though historians' accounts of British interwar genetics only give a view of the important men and their achievements, some scientists have written recollections that have been useful for my work. The most helpful of these are D. Lewis's description of the origin, changing membership, and discussions of the Genetical

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<sup>87</sup> Palladino, 2002, chapters two and three.

<sup>88</sup> Palladino, 2002, chapters four and five.

<sup>89</sup> Olby, 1991a.

Society;<sup>90</sup> and F.A.E. Crew's description of genetics in Britain under Bateson, his recollections of Genetical Society meetings up to 1942, and acceptance of the chromosome theory in Britain from the 1920s as indicated by cytological discussions at the Genetical Society.<sup>91</sup> Crew has also written a history of the Edinburgh genetics department from 1882 to 1939, concentrating on the period from 1920.<sup>92</sup> Brief histories of the Edinburgh department of genetics also exist on the Internet<sup>93</sup> and an unpublished history is available in the department's archives.<sup>94</sup> Similar resources exist for the JI,<sup>95</sup> but this has been less important for my dissertation.

## 1.11 Intellectual Background

In this section I outline the main findings that had been made in the different research areas of genetics by the start of the 1930s. This shows what intellectual traditions geneticists in the 1930s were drawing upon.

### 1.11.1 Transmission Genetics

By 1930 the theory that genes were on chromosomes was generally accepted by geneticists. In 1915, T.H. Morgan and students had published the results of their work on *Drosophila melanogaster*.<sup>96</sup> They argued that linkage arose from two genes being on the same chromosome, and showed that the number of linkage groups in *Drosophila* matched the number of chromosome pairs it had. They also argued that two linked genes could segregate from each other, when the chromosomes exchanged material during crossing-over. By studying the frequency at which this occurred the relative distance between genes could be established. This argument formed the basis of genetics during the 1930s. In evolutionary genetics the homology of chromosomes between species was investigated, to find out how the species evolved, by the creation and comparison

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<sup>90</sup> Lewis, 1969.

<sup>91</sup> Crew, 1969.

<sup>92</sup> Crew, 1971.

<sup>93</sup> McKeen, 2002. Bulfield, 1999.

<sup>94</sup> Deacon, unpublished.

<sup>95</sup> Scott-Moncrieff, 1981, Lawrence, 1962 and Lawrence, 1980.

<sup>96</sup> Morgan, Sturtevant, Muller and Bridges, 1915. Kohler, 1994.

of gene maps for different species. In physiological/developmental genetics, it was established whether alleles with similar phenotypic effects were allelomorphic or affected the same physiological process by mapping them onto chromosomes.

During the 1920s, however, the chromosome theory still faced some difficulties. One of these was the belief amongst botanical cytologists that the chromosomes paired end to end during synapsis (telosynapsis) rather than length-ways (parasynapsis). If this was true, the chromosomes would have little chance to swap material by crossing-over.<sup>97</sup> The problem of synapsis dominated cytogenetic research during the 1920s in Britain. In 1920 Lancelot Hogben demonstrated parasynapsis in cockroaches.<sup>98</sup> During the 1920s Frank Newton and Cyril Darlington worked at the JI to show that parasynapsis also occurred in plants. The course of Darlington's investigation led him to suggest that chromosome pairing occurred by means of chiasmata. In 1932 Darlington went on to suggest that chiasmata result from crossing-over.<sup>99</sup> Darlington's was not the only theory of the relationship between crossing-over and chiasmata. In 1930 Karl Sax suggested that crossing-over was the result of chiasmata breaking.<sup>100</sup> Deciding between the two became an important issue for cytogeneticists during the 1930s.

Further evidence for the material nature of the gene came from H.J. Muller's 1927 announcement that X-rays could cause mutations.<sup>101</sup> As Dunn has pointed out, if gene changes could be affected by material changes, it was likely that genes were also materialistic.<sup>102</sup> Muller's discovery affected many branches of genetics. During the 1930s, evolutionary geneticists used X-rays to promote mutations. These could then be mapped and the maps compared to establish homologies. It led to investigations into the mechanics of how mutations occurred, as described in Chapter Five (section 5.4.2). X-rays were also used to promote chromosomal changes so that position effects could be studied.

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<sup>97</sup> Wells, 1978, 190.

<sup>98</sup> Hogben, 1920.

<sup>99</sup> Darlington, 1998, 70-72.

<sup>100</sup> Sax, 1930, 216-217.

<sup>101</sup> Muller, 1927.

<sup>102</sup> Dunn, 1965, 132.



Position effect was the idea that a gene's phenotype is dependent upon the position of the gene to other genes on the same chromosome. The idea was first suggested by A.H. Sturtevant in 1925. It became easier to investigate during the 1930s. Not only could X-rays be used to promote chromosome changes, but in 1933 T. Painter discovered the giant salivary gland chromosomes. These enabled chromosomal changes to be correlated with phenotypic changes. They also led Painter to suggest that genes were on the darkly staining bands of the chromosomes.<sup>103</sup>

### 1.11.2 Physiological/Developmental Genetics

In 1902 A. Garrod suggested that the gene for alkaptonuria acted via an enzyme deficiency or inactivity. In Britain this was followed up first by Muriel Wheldale in 1914, who investigated the relationship between the inheritance of flower colour and the inheritance of anthocyanin.<sup>104</sup> In 1926 Whedale encouraged the British biochemist, Rose Scott-Moncrieff, to investigate this problem further. During the 1930s Scott-Moncrieff did so in collaboration with W.J.C. Lawrence, of the JI, and Oxford University chemists, who were trying to synthesise anthocyanins.<sup>105</sup> The main approach to physiological genetics in 1930s Britain was a comparison of the genetics behind different physiological traits. A discussion of such studies at the DoZ/B is given in Chapter Four (section 4.4.2.2).

During the 1920s a new approach to the problem arose. In 1920 Sturtevant suggested that gene products were diffusible, after showing that the male tissues of a gynandromorph expressed the phenotype of genes that were in its female tissues, but not in its male ones.<sup>106</sup> This led onto transplant studies, such as Beadle and Ephrussi's experiments with *Drosophila* eye-colour, during the 1930s.

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<sup>103</sup> Dunn, 1965, 161-163. Painter, 1933.

<sup>104</sup> Wheldale, 1914/1915, 109.

<sup>105</sup> Scott-Moncrieff, 1981, 127.

<sup>106</sup> Dunn, 1965, 177.

In 1916 R. Goldschmidt proposed the balance theory of sexuality. Goldschmidt had found that when European and Japanese races of gypsy moths (*Lymantria*) were crossed, intersexes were always formed. He suggested that the extent of intersexuality was determined by the balance between the male determining factor on the X chromosome and the female determining factor on the Y-chromosome. The strength of these factors varied between the races. Goldschmidt also proposed that intersexes develop as one gender until a turning point is reached when they develop as the other gender. The gender of an individual organ is determined by whether the female or male process proceeds most rapidly at the critical period for determining the gender of the organ.<sup>107</sup> Goldschmidt developed this idea into a more general theory that genes acted by controlling the rates of reactions.<sup>108</sup>

### 1.11.3 Population/Evolutionary Genetics

In 1908 G.H. Hardy and W. Weinberg independently showed that the frequencies at which alleles occurred in a randomly-mating population would be in equilibrium. The most influential work on 1930s population genetics was the mathematical work of S. Wright, R.A. Fisher and J.B.S. Haldane. During the early 1920s Wright investigated the effects that inbreeding had on the genetics of populations. At the end of the 1920s Fisher investigated the effects of selection on the genetics of populations and the idea that dominance evolved. Throughout the 1920s Haldane estimated the equilibrium that was attained when new alleles were introduced by mutations and then selected against.<sup>109</sup>

In 1926 S.S. Chetiverikov suggested that wild populations store mutations heterozygously, which produced the variability to deal with changing conditions. He and his students captured *Drosophila melanogaster* and inbred them, to reveal the extent to which recessive alleles were retained in the population

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<sup>107</sup> Allen, 1974. Sinnott and Dunn, 1932, 218-219.

<sup>108</sup> Harwood, 1993, 51-52. Dunn, 1965, 188.

<sup>109</sup> Provine, 1971, 131-136, 140-176.

heterozygously. This work was repeated by members of the DoZ/B during the 1930s.<sup>110</sup>

## **1.12 Conclusion**

In this chapter I have discussed the theses that underlie this dissertation, the main models I use and the literature that is already published in the field. In my next chapter I will provide a location-focused history of British genetics between 1900 and 1940 to examine my first thesis that genetics was growing at different rates in the different settings there were for it during the 1930s. This will also provide a framework by which previous histories of British geneticists and their work can be integrated, and it will provide the context for the rest of my study. I will also look in more detail at the DoZ/B at UCL and the IAG at the UoE. I will use the definitions of different settings, provided in section 1.5, to demonstrate that these locations belonged to the academic and agricultural settings respectively. This classification provides the basis for the comparisons made in the rest of this dissertation.

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<sup>110</sup> Adams, 1968.

## **Chapter Two**

### **The Department of Zoology/Biometry and the Institute of Animal Genetics as Locations for British Genetics**

#### **2.1 Introduction**

In this chapter (sections 2.2 and 2.3) I discuss the histories of the Department of Zoology/Biometry (DoZ/B) at University College London (UCL) and the Institute of Animal Genetics (IAG) at the University of Edinburgh (UoE), to demonstrate that they belonged to the academic and breeding settings respectively. This enables me to use my comparisons of genetics at these two locations as the basis for comparing genetics in the two settings. My descriptions of the two locations will also provide the necessary background for gaining a full understanding of the analysis presented in the rest of this thesis. In discussing the two locations I will synthesise previous histories and draw on a variety of archival sources to provide exemplars of locations in the British academic and breeding settings during the 1930s.

Following this, in section 2.4, I provide a history of British genetics to 1940. This contextualises the locations and demonstrates my first thesis that genetics grew at different rates across the different settings in 1930s Britain. This history synthesises biographies, histories of genetics and published genetics papers to provide a context for the histories of British geneticists or individual research projects in Britain that already exist for this period. Furthermore, I argue that the history of British genetics cannot be fully understood without a consideration of setting. This history provides a framework for the formation of such a history.

Finally in this chapter, I consider how representative the two locations were of their respective settings in section 2.5. This reveals the degree of homogeneity in the settings and what considerations there must be when expanding my findings from locations to settings. This section synthesizes histories of genetics and agriculture with some archival material to provide a better understanding of the settings during the 1930s.

## 2.2 The DoZ/B, UCL

This section discusses the history of genetics at the Department of Zoology (DoZ), later the Department of Biometry (DoB), at UCL to 1945. This provides the context for the analyses provided in future chapters. More importantly, it demonstrates that the Department was in the academic setting. This description therefore also acts as an exemplar of locations in the academic setting.

### 2.2.1 Reshaping the DoZ

In 1921 the palaeontologist, D.M.S. Watson, became head of the DoZ at UCL. By 1925 Watson had a vision of the DoZ where experimental zoologists worked alongside descriptive zoologists to gain a greater understanding of animals' structure and function, and especially of evolution. Watson appears to have been motivated in part by disciplinary considerations. He was a palaeontologist and thus a descriptive zoologist. However, during the 1920s zoologists were beginning to turn away from descriptive methods.<sup>111</sup> Watson wrote that palaeontology still had much to offer the discipline of zoology. He stated that he would have more influence over experimentalists if some worked alongside him in the department.<sup>112</sup> Watson was also motivated by the belief that experimental zoology offered exciting new results and that experimental subjects such as genetics, experimental embryology and physiology would benefit from being synthesised with each other and palaeontology.<sup>113</sup>

One barrier to Watson's vision was the Department's poor accommodation.<sup>114</sup> Lectures were held in a steeply inclined theatre. The top of the theatre was boarded off to form the senior laboratory and research rooms.

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<sup>111</sup> Benson, 1991 discusses the move towards laboratory science in America.

<sup>112</sup> Watson to Osborn, 15 September 1925, f432, b30, s2, IEBA.

<sup>113</sup> "The Policy of the Zoological Department of UCL," 7 February 1927, f433, b30, s2, IEBA.

<sup>114</sup> Watson to Osborn, 15 September 1925, f432, b30, s2, IEBA. Doctor Lillie's Report, March 21, 1926, f432, b30, s2, IEBA. A4, MS. ADD. 386, Watson papers.

At the same time Watson became head of the DoZ, the International Education Board (IEB)<sup>115</sup> were funding the expansion of the Anatomy, Physiology and Pharmacology Departments at UCL.<sup>116</sup> The head of the Anatomy Department, Grafton Elliot Smith, encouraged Watson to turn to the Rockefeller philanthropies for aid.<sup>117</sup>

The IEB was not initially interested in funding the department. It was interested in “making the peaks higher” in the European university system.<sup>118</sup> This meant funding the best scientists who were already in established positions. In 1925 the IEB did not view Watson as an excellent zoologist and they were being asked to fund the establishment of a top laboratory rather than support an already existing one. Such a request was viewed as one to expand UCL so it could employ more top scientists rather than a request to support the work of a top scientist.<sup>119</sup> Kohler has argued it was against IEB policy to support scientists that were not top-rank because improvements in their departments would inevitably involve them losing power to the scientists brought in. It would therefore not be in the interest of such scientists to improve.<sup>120</sup>

The Board was interested in improving university zoology in Britain, however. The Board identified the peaks in a discipline by asking travelling professors to report on the state of their discipline in the countries they visited.<sup>121</sup> In 1926 the American biologist, F.R. Lillie, reported on British zoology to the Board. Lillie concluded that there were three main zoology laboratories in Britain, located at King’s College, London, Imperial College, London and UCL. Lillie stated that there were no outstanding zoologists but that the most impressive was probably Watson. He recommended the establishment of an experimental zoology institute in London. Lillie wrote that this would be best situated at UCL. He also stated

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<sup>115</sup> The IEB was one of the Rockefeller philanthropies. It particularly funded scientific higher education outside the United States. (The Rockefeller philanthropy, The General Education Board, funded scientific higher education inside the United States.)

<sup>116</sup> For details see Fisher (Donald), 1978.

<sup>117</sup> Purchase of Shoolbred’s Mews by UCL, MS. ADD. 341, Watson papers.

<sup>118</sup> Kohler, 1991a, 163.

<sup>119</sup> AF:ESB September 21, 1925, f432, b30, s2, IEBA.

<sup>120</sup> Kohler, 1991a, 164.

<sup>121</sup> Kohler, 1991a, 148.

that the institute could probably be achieved by developing the existing DoZ.<sup>122</sup> UCL therefore became identified as a peak in British zoology by the IEB in 1926 and thus talks between the Board and Watson resumed.

Watson's vision of the department developed from a general one of experimentalists working with descriptive zoologists<sup>123</sup> into a more specific vision by 1927.<sup>124</sup> The vision was of a department staffed by Watson as a palaeontologist, a geneticist, a comparative physiologist, a cytologist, an animal behaviourist, a morphologist and a chemist. Of the geneticist he hoped to employ, Watson wrote:

“I feel that the small interest which British Zoologists have displayed in the fundamental subject of Genetics renders it very desirable that the department should include a geneticist of the first rank. There is no man available in Britain, and I should hope to attract one from the Columbian school.”<sup>125</sup>

The Columbian zoologist, Gary Calkins, who also surveyed zoology for the IEB,<sup>126</sup> approached the Columbian geneticist, A.H. Sturtevant, regarding the geneticist job on Watson's behalf in January 1927.<sup>127</sup> Although Sturtevant was interested, nothing came of it.

Nevertheless, in May 1927 the IEB agreed to provide £120,000 towards new accommodation and staff for the Department on the condition that the College raised matching funds for the project.<sup>128</sup> By 1931, when Britain was in the middle of the Great Depression, it was clear that the College could not raise matching funds and so the Board terminated the agreement.<sup>129</sup>

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<sup>122</sup> Supplementary Report by F.R. Lillie, March 8-23, 1926, f432, b30, s2, IEBA.

<sup>123</sup> Statement by D. M. S. Watson of the reasons which render necessary the provision of a new building for the DoZ at UCL, f432, b30, s2, IEBA.

<sup>124</sup> The Policy of the Zoological Department of UCL, February 7, 1927, f433, b30, s2, IEBA.

<sup>125</sup> The Policy of the Zoological Department of UCL, February 7, 1927, f433, b30, s2, IEBA.

<sup>126</sup> Kohler, 1991a, 149.

<sup>127</sup> Calkins to Watson, 25 February 1927, B6, MS. ADD. 386, Watson papers.

<sup>128</sup> Brierley to Foster, June 28, 1927, f434, b30, s2, IEBA. UCL, DoZ and Comparative Anatomy, 12 December 1930, f435, b30, s2, IEBA.

<sup>129</sup> UCL, DoZ and Comparative Anatomy, 12 December 1930, f435, b30, s2, IEBA. Brierley to Mawer, April 22, 1931, f435, b30, s2, IEBA.

UCL submitted a new, reduced, proposal to the Natural Sciences Division (NS) of the Rockefeller Foundation (RF) in 1931.<sup>130</sup> The proposal shows that Watson's vision had hardly changed. He pointed out the need for two comparative physiologists, a genetical physiologist, an animal behaviourist and a morphologist in the department. However, Watson prioritised the employment of a comparative physiologist and an animal behaviourist (a morphologist was already employed). He planned to train people for the other posts. Comparative physiology and animal behaviour were therefore highlighted as the fields most important to his vision.<sup>131</sup>

In December 1931 the RF awarded UCL £88,000 for the new proposal on the condition that the £30,000 already raised for the Department was put towards building and maintenance costs. The agreement did not include provision for a geneticist. However, the plans were intended to make the department more experimental in terms of both staff research interests and the facilities available.

Though there was no provision for a geneticist, Watson asked the geneticist and biochemist, J.B.S. Haldane, if he would lecture in the department. This resulted in Haldane's employment part-time as a professor of genetics at the start of 1933.<sup>132</sup> The employment of a professor in the Department was part of the plan Watson submitted to the IEB in 1931.<sup>133</sup> However, according to that plan, the professor was to be in comparative physiology. It is possible that the RF was responsible for the suggestion that another professor was employed in the department. In his report to the Board, Lillie wrote:

“Watson is a fine person, but more palaeontologist than zoologist, and the question of associating another professor with him should come up in case of considering any large developments.”<sup>134</sup>

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<sup>130</sup> The IEB passed out of existence at the end of 1928, as the Rockefeller philanthropies consolidated. This is discussed more in Chapter Three (section 3.2). The NS of the RF took over funding university science at this time.

<sup>131</sup> Memorandum on the Present Condition of Zoological Studies and the Opportunities which Present Themselves for their Development at UCL, f589, b46, s401D, RFA.

<sup>132</sup> Watson to Medawar, 11 January 1957, folder MS. ADD. 112/1 (2), Watson papers.

<sup>133</sup> Memorandum on the Present Condition of Zoological Studies and the Opportunities which Present Themselves for their Development at UCL, f589, b46, s401D, RFA.

<sup>134</sup> Doctor Lillie's Report, March 21, 1926, f432, b30, s2, IEBA.



Whether Haldane's professorship was intended by Watson and Haldane to be permanent is not clear. At the time, Haldane was expecting to succeed A.D. Hall to the directorship of the John Innes Horticultural Institution (JI). This suggests that he only intended to hold the post at UCL temporarily. However, Watson stated that Haldane was interested in the post because he could not teach at the JI.<sup>135</sup> This would not have changed upon his succession to the Directorship. Furthermore, in 1934 Haldane reportedly said he would probably remain at UCL as well as directing the JI until genetics was properly established.<sup>136</sup>

Whatever the long-term plan, Haldane began work in the DoZ in 1933.<sup>137</sup> The result of the Rockefeller's support for Watson's vision was that the department's focus changed from being exclusively concerned with structure to combining this interest with function. Around 1933 the cytologist, M.J.D. White, was employed on a three year contract<sup>138</sup> and E.S. Russell agreed to lecture on animal behaviour.<sup>139</sup> G.P. Wells and N.H. Howes were already employed by then as comparative physiologists,<sup>140</sup> as was Elizabeth Fraser as an embryologist.<sup>141</sup>

In March 1933 the DoZ began to move into their new building and in June it was officially opened. The new building was approximately twice the size of the department's old accommodation and had constant temperature rooms, an animal house and an aquarium.<sup>142</sup> Plans of the building are given in Appendix One. The building was paid for by the RF because it would enable research on animal functions to occur at UCL. There is evidence that the new facilities greatly improved the staff's ability to do such work. In the summer of 1933 the

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<sup>135</sup> Watson to Medawar, 11 January 1957, folder MS. ADD. 112/1 (2), Watson papers.

<sup>136</sup> Miller's diary, March 14-15, 1934, RG 12.1, RFA.

<sup>137</sup> Watson to Medawar, 11 January 1957, folder MS. ADD. 112/1 (2), Watson papers. Weaver's diary, November 30, 1932, RG 12.1, RFA. *The Department of Zoology and Comparative Anatomy*, 1933, 4.

<sup>138</sup> Miller's diary, November 17, 1932, RG 12.1, RFA. Miller's diary, March 13, 1935, RG 12.1, RFA.

<sup>139</sup> *The Department of Zoology and Comparative Anatomy*, 1933, 5.

<sup>140</sup> *The Department of Zoology and Comparative Anatomy*, 1933, 2. A4, MS. ADD. 386, Watson papers. A1, *The Times* 25 July 1973, MS ADD 386, Watson papers.

<sup>141</sup> *The Department of Zoology and Comparative Anatomy*, 1933, 2. Parrington and Westoll, 1974, 487.

<sup>142</sup> Jones's diary, March 2, 1933, RG 12.1, RFA. *The Department of Zoology and Comparative Anatomy*, 1933.

physiologist, M. Graubard, complained that the heat made *Drosophila* work in the department impossible.<sup>143</sup> The constant temperature rooms were not then in operation.<sup>144</sup> The animal house also did not open until Christmas 1934. Its opening was given by the geneticist, Hans Grüneberg, as a possible reason for the improvement in one of his mouse stocks.<sup>145</sup>

By the end of 1933 the facilities and staff were in place for the implementation of Watson's vision of zoology at UCL. Constant temperature rooms, an aquarium and an animal house were all in the process of being built, if not already open. Experimentalists, including two comparative physiologists, a geneticist, a cytologist, an animal behaviourist and an embryologist, were employed alongside Watson. The most important positions for his vision (comparative physiology and animal behaviour) had been filled. However, as is discussed in the next section, Watson's vision was not fulfilled quite as he had planned. There were two main reasons for this: the geneticist he employed, J.B.S. Haldane, was highly regarded and so attracted funds that skewed the department towards genetic studies and secondly, Haldane had a vision of his own.

### 2.2.2 From Geneticist to Genetics Group

Prior his employment at the DoZ, Haldane developed a research programme for genetics in the Department and acquired the necessary techniques and research materials to implement it. In 1932 Haldane learnt *Drosophila* genetics techniques at the centre for such studies, T.H. Morgan's laboratory at Caltech. Haldane told the mouse geneticist, L.C. Dunn, that he would use the techniques to conduct experimental population studies.<sup>146</sup> Haldane also collected several strains of mice while in America, which he took back with him to UCL.<sup>147</sup> These, he told Dunn, he would use to compare the physiology and pharmacology of different lines. He also intended to investigate the serological differences

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<sup>143</sup> Miller's diary, June 12, 1933, RG 12.1, RFA.

<sup>144</sup> The Department of Zoology and Comparative Anatomy, 1933, 6.

<sup>145</sup> Grüneberg, 1938b, 159.

<sup>146</sup> Haldane to Dunn, October 10, [1932], folder Haldane, J.B.S., Dunn papers.

<sup>147</sup> Haldane to Dunn, November 9, [1932], folder Haldane, J.B.S., Dunn papers. Haldane to Dunn, July [1933], folder Haldane, J.B.S., Dunn papers.

between strains and conduct a three point linkage test.<sup>148</sup> Before beginning work at UCL Haldane therefore had a vision of genetics at the location and he had acquired the necessary techniques and materials for the work.

In many ways Haldane's vision of genetics at UCL fitted Watson's vision of the department. In his 1926 statement of why a new building was necessary, Watson stated that his recent conclusions about evolution seemed to fit well with the conclusions of geneticists and experimental embryologists. Watson wanted to carry out experiments on the development of animals to further his own conclusions about evolution.<sup>149</sup> Haldane's research programme prioritised experimental population genetics, which experimentally investigated evolution from a genetic perspective. Haldane also planned to investigate the function of animals genetically. This fitted well with Watson's plan to combine investigations of structure and function in the department.<sup>150</sup>

Haldane's vision required other researchers, especially as Haldane was not really capable of experimental research himself.<sup>151</sup> Since there was no money for additional staff, Haldane probably envisaged these researchers as students and maybe a few researchers on temporary grants. The staff he acquired were an *ad hoc* collection of PhD students, refugees, visitors and a few miscellaneous researchers.

The first geneticists to join him in the Department were Hans Grüneberg and Ursula Philip, in August 1933.<sup>152</sup> Haldane invited the pair to the Department in

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<sup>148</sup> Haldane to Dunn, October 10, [1932], folder Haldane, J.B.S., Dunn papers. Haldane had already acquired funding for Peter Gorer to perform similar serological tests on fowls at the JI by this time (see below).

<sup>149</sup> Statement by D. M. S. Watson of the reasons which render necessary the provision of a new building for the DoZ at UCL, f432, b30, s2, IEBA.

<sup>150</sup> The Policy of the Zoological Department of UCL, f433, b30, s2, IEBA.

<sup>151</sup> Miller's diary, December 5, 1934, RG 12.1, RFA. Tisdale's diary, March 9-11, 1936, f579, b45, s401D, RG 1.1, RFA.

<sup>152</sup> Lewis and Hunt, 1984, 229 states that Grüneberg began work in August 1933. Since the funding for Grüneberg and Philip came through at the same time it seems likely that Philip also began work in August. A female German refugee was working at the department in September (Miller's diary, September 26, 1933, RG 12.1, RFA). Philip is recorded as being at the DoZ in December 1933 (Miller's diary, December 13, 1933, RG 12.1, RFA).

June 1933,<sup>153</sup> following the dismissal of Jews from university posts in Germany.<sup>154</sup> He obtained emergency grants to support them for two years from the Central British Fund for German Jewry.<sup>155</sup> Philip began work on crossing over between the sex chromosomes of *Drosophila*,<sup>156</sup> which was outside Haldane's program if it is viewed in a narrow sense. The problem had implications regarding the evolution of gender however. The work also drew on Philip's background as a *Drosophilist*.<sup>157</sup> Grüneberg began to conduct the three point linkage test that Haldane had planned with mice<sup>158</sup> and, in all likelihood, research on the mutations caused in *Drosophila* by X-rays.<sup>159</sup> This also related to Grüneberg's previous experience<sup>160</sup> and to evolutionary questions. X-rays could be used to see which genes were on different chromosomes. If this was done for a variety of species, the chromosomes could be compared for homology, which revealed how closely related the species were.<sup>161</sup>

Grüneberg and Philip were joined by the geneticist, Peter Gorer, in 1933/1934. In 1933 the Medical Research Council (MRC) awarded Gorer research expenses for a genetic investigation of serological differences in fowl to be conducted at the JI.<sup>162</sup> However, research on the project did not progress very far.<sup>163</sup> By March 1934 he was investigating serological differences between strains of mice at the DoZ without funding.<sup>164</sup> There is no evidence regarding Gorer's move to UCL, but I would suggest that the work Gorer intended to conduct at the JI was so close to the research Haldane planned to do at UCL that he persuaded Gorer to work at UCL on mice instead. By March 1934 Cecil Gordon was also researching genetics in the Department.<sup>165</sup> Gordon was a PhD student who

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<sup>153</sup> Lewis and Hunt, 1984, 229 states that Grüneberg received his invite in June. It seems likely that Haldane invited Philip at the same time.

<sup>154</sup> Deichmann, 1996b, 11.

<sup>155</sup> The Joint Foreign Committee, Woburn House to Grüneberg, 10 August 1933, folder Pm-Q, b13, Grüneberg papers.

<sup>156</sup> Miller's diary, March 14-15, 1934, RG 12.1, RFA.

<sup>157</sup> For a discussion of this research see Chapter Five. For Philip's background see Miller's diary, March 14-15, 1934, RG 12.1, RFA.

<sup>158</sup> Lewis and Hunt, 1984, 232.

<sup>159</sup> Grüneberg, 1935b.

<sup>160</sup> Lewis and Hunt, 1984, 231.

<sup>161</sup> For a discussion of this research see Chapter Five.

<sup>162</sup> GTI to Gorer, 3 May 1933, folder FD 1/3297, MRC papers.

<sup>163</sup> Gorer to Sir, 14 June 1934, folder FD 1/3287, MRC papers.

<sup>164</sup> Miller's diary, March 14-15, 1934, RG 12.1, RFA.

<sup>165</sup> Miller's diary, March 14-15, 1934, RG 12.1, RFA.

undertook experimental population genetics work in the department.<sup>166</sup> This again matched Haldane's planned programme of research.

By the end of 1934 the group had enlarged to also include Pius Koller, Pierre Lafon, F.C. Minns and A.L.M. Christie. Christie was a PhD student who researched what lethal mutations arose in the autosomes of *Drosophila* when they were exposed to X-ray radiation.<sup>167</sup> As discussed for Grüneberg above, this work had evolutionary significance. Minns was still studying for the Cambridge tripos, but at UCL he researched preferential mating in *Drosophila* bred in the dark.<sup>168</sup> This work was also relevant to evolutionary questions. Lafon had a Caisse Nationale grant to work with Haldane at UCL for a year.<sup>169</sup> While there he worked on haemoglobin differences between strains of mice.<sup>170</sup> This fitted Haldane's plan of investigating physiological differences between mouse strains.

Koller had previously worked at the IAG, but in August 1934 he decided he could not remain there due to their shortage of funds. Haldane had previously offered him bench space and he now took up the offer.<sup>171</sup> Though Koller gained work space at UCL, Haldane had no funding for him. Instead he lodged with the cytologist, Cyril Darlington, and Haldane paid his board.<sup>172</sup> Koller worked on two projects.<sup>173</sup> One studied the pairing of the X and Y chromosomes during meiosis in monkeys. The importance of the work was that Darlington had associated pairing with chiasmata and chiasmata with crossing over. Uncontrolled crossing over in the sex chromosomes would cause the X and Y chromosomes to become increasingly similar to each other. If this occurred the differentiation of the genders would cease. This work therefore approached the same problem Philip was studying genetically, from a cytological viewpoint. The other problem had more direct evolutionary relevance. Koller studied the

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<sup>166</sup> Gordon, 1936, 56.

<sup>167</sup> Miller's diary, October 22, 1934, RG 12.1, RFA.

<sup>168</sup> Miller's diary, October 22, 1934, RG 12.1, RFA.

<sup>169</sup> Miller's diary, October 22, 1934, RG 12.1, RFA.

<sup>170</sup> Miller's diary, October 22, 1934, RG 12.1, RFA.

<sup>171</sup> Koller to Darlington, 14 August 1934, folder J.122, box c.110, Darlington papers.

<sup>172</sup> Miller's diary, October 22, 1934, RG 12.1, RFA. Haldane to Miller, October 3, 1934, f578, b45, s401D, RG 1.1, RFA.

<sup>173</sup> Summary of Work in Progress, 3 October 1934, f578, b45, s401D, RG1.1, RFA. See also Miller's diary, October 22, 1934, RG 12.1, RFA. Both projects are described in detail in Chapter Five.

cytology of different races of *Drosophila pseudo-obscura*. This accounted for the partial sterility that existed between the races and thus helped explain the formation of new species.

By the end of 1934 there was therefore a group of eight geneticists working with Haldane at UCL. None had permanent positions in the Department. Two were PhD students, two were refugees with impermanent funding, two were researchers without funding, one was a visitor and one was still studying for his undergraduate degree. While these researchers appear to have come together in an *ad hoc* manner they were bound by their interest in different parts of Haldane's research programme. Of the researchers, five were doing research directly relating to Haldane's planned research programme: Grüneberg, Gorer, Gordon, Lafon and Koller. The work of Philip, Minns and Christie also had implications regarding the genetics of evolution.<sup>174</sup>

Both Watson's vision of the Department and Haldane's vision of genetics guided the genetics research done there. Due to Watson's vision there were the facilities for experimental work and Haldane to guide it. Due to Haldane's vision, the research focused on experimental population genetics and physiological genetics. Haldane's vision had more specific impact than Watson's. However, the research that was done went beyond Haldane's vision. Even those problems that fitted Haldane's programme well, such as Lafon's, had input from the individual that carried out the research. In Lafon's case he chose what physiological trait to compare.

While Haldane's vision was implemented, the temporary nature of the researchers who worked around him threatened the stability of this realisation. In the next section I therefore look at how Haldane tried to maintain his group.

### 2.2.3 Maintaining the Group

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<sup>174</sup> While most of the work fitted Haldane's planned programme of research, other work also arose during the course of the investigations. For example, Grüneberg investigated a chromosomal inversion in *Drosophila* caused by X-ray radiation. (Grüneberg, 1935b). For more details of this work see Chapter Five (section 5.4.1.2).

The formation of a genetics group in the DoZ enabled Haldane to exceed the programme of research he planned in 1932. However, it put Haldane in the position of being responsible for eight geneticists, none of whom had permanent funding.

This was not a problem for Gorer, Lafon, Minns and Christie. In 1934 Gorer joined the Lister Institute and reduced his work at UCL to part-time. Lafon had a grant to visit UCL while Minns and Christie were students. The main problems were Grüneberg, Philip, Koller and Gordon. Grüneberg and Philip's emergency funding ran out in July 1935, Koller had no funding and Gordon's PhD grant terminated in December 1934.<sup>175</sup> In October 1934 Haldane wrote to the Rockefeller officer, H.M. Miller:

“My real trouble, as you know, is not shortage of material (though we could do with more) but of salaries.”<sup>176</sup>

At the end of 1934, the immediate problem was paying Koller and Gordon, both of whom Haldane wanted to retain. Haldane also wished to retain Philip at that time.<sup>177</sup> There is no evidence for why this was. However the specialities of these three individuals suggest that Haldane wished to focus on *Drosophila* population genetics. Philip was perceived as an expert *Drosophila* geneticist. Gordon was working on experimental population genetics with *Drosophila*. Koller was a cytologist, who was then comparing the chromosomes of different races of *Drosophila*. Koller's research helped to explain the establishment of the races and their possible evolution into species.

Haldane turned to the RF for help securing their employment. The Foundation granted aid to Haldane for a year in March 1935. The award paid Gordon to work on *Drosophila* population genetics and Koller to work on the cytology of inter-racial hybrids of *Drosophila*. The money also allowed Haldane to purchase the

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<sup>175</sup> Haldane to Miller, October 3, 1934, f578, b45, s401D, RG 1.1, RFA.

<sup>176</sup> Haldane to Miller, October 3, 1934, f578, b45, s401D, RG 1.1, RFA.

<sup>177</sup> Miller's diary, October 22, 1934, RG 12.1, RFA.

equipment they required for this research.<sup>178</sup> The Rockefeller's interest was in Haldane, of whom they wrote:

“J.B.S. Haldane and R.A. Fisher are the only two geneticists with real possibilities in Europe today. NS must eventually enter into genetics activities with these two scientists.”<sup>179</sup>

Though Haldane had told the Foundation that he would remain at UCL when appointed Director of the JI,<sup>180</sup> the situation was not clear until that happened. The grant they made therefore supported work they thought would be completed within a year.<sup>181</sup>

In mid-1935 Grüneberg and Philip's funding became an issue. Haldane persuaded the Professional Committee for German Jewish Refugees<sup>182</sup> to extend their funding until the end of November 1935.<sup>183</sup> Haldane was not very keen to retain Grüneberg but, as discussed above, he wanted to retain Philip.<sup>184</sup> Haldane intended to ask the College to allocate £200 from his wage to provide Philip with a permanent post once he was appointed Director of the JI.<sup>185</sup>

At the end of 1935 Haldane turned once more to the RF for help supporting Grüneberg and Philip.<sup>186</sup> The Foundation encouraged Haldane to plan a permanent programme of genetics research in the department.<sup>187</sup> During 1936, while Haldane formed such a plan, the Foundation provided salaries for his staff.<sup>188</sup> During 1934/1935 Haldane maintained his group of geneticists through crisis management. In 1936 Haldane began to plan the stabilisation of his group for a number of years.

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<sup>178</sup> Research Aid Grant, NS Paris R.A. Action No. 4, f578, b45, s401D, RG 1.1, RFA.

<sup>179</sup> Form 212, Tisdale to Weaver, November 17, 1934, f578, b45, s401D, RG 1.1, RFA.

<sup>180</sup> Miller's diary, March 14-15, 1934, RG 12.1, RFA.

<sup>181</sup> Grant in aid, Paris R. A. Action No. 4, January 7, 1935, f578, b45, s401D, RG 1.1, RFA.

<sup>182</sup> Previously the Central British Fund for German Jewry.

<sup>183</sup> Professional Committee for German Jewish Refugees to Grüneberg, 16 July 1935, folder Pm-Q, b13, Grüneberg papers. Tisdale's diary, July 5, 1935, RG 12.1, RFA.

<sup>184</sup> Miller's diary, October 22, 1934, RG 12.1, RFA.

<sup>185</sup> Tisdale's diary, 5 September 1935, f578, b45, s401D, RG 1.1, RFA.

<sup>186</sup> Koller left the Department in March 1935 and Gordon gained funding from the Royal Society during 1935. See Chapter Three (section 3.3.1).

<sup>187</sup> Tisdale to Weaver, December 17, 1935, f578, b45, s401D, RG 1.1, RFA.

<sup>188</sup> Grant in aid 35254, f578, b45, s401D, RG 1.1, RFA.



These plans ran into trouble in June/July 1936, however, when Haldane discovered that he was not going to be appointed Director of the JI as expected.<sup>189</sup> Haldane began looking for a new job, focusing his attention on the United States.<sup>190</sup> Thus while Haldane successfully managed to keep his researchers throughout 1935 and the start of 1936, the group was threatened in mid-1936 by the possibility of Haldane leaving UCL. In the next section I look at the steps Watson took to ensure Haldane stayed in the department.

#### **2.2.4 The DoB**

In 1936 the widow of the biometrician, W.F.R. Weldon, died. In her Will there was a legacy to endow a chair of biometry, preferably at UCL. Mrs Weldon intended the professor to work in the Galton Laboratory in close collaboration with the Galton professor.<sup>191</sup> This caused a problem for UCL. The Galton Laboratory had been split into two departments in 1932: Eugenics and Statistics. The College had appointed the mathematical population geneticist, R.A. Fisher, Galton professor at that time. A year later it had created a professorship for the head of the statistics department, Egon Pearson. During the 1930s petty fighting occurred between Fisher and Pearson. This made awarding Pearson the Weldon professorship difficult, especially as he already had a professorship.

The suggestion arose that Haldane be awarded the Weldon professorship to secure his position at UCL. In some ways Haldane's appointment to the position made sense. Haldane and Fisher were on good terms in 1936. Haldane was in fact collaborating quite extensively with one of Fisher's staff, Julia Bell.<sup>192</sup> In other ways it was not obvious. Haldane led a group of geneticists whose focus was genetics and not biometry. By the end of 1936, however, UCL had decided to offer the chair to Haldane. Watson appears to have played a part in the

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<sup>189</sup> WET-WW, June 12, 1936, f579, b45, s401D, RG 1.1, RFA. Miller's diary, July 9-10, 1936, RG 12.1, RFA.

<sup>190</sup> Miller's diary, July 9-10, 1936, RG 12.1, RFA. Hanson's diary, August 5, 1936, RG 12.1, RFA.

<sup>191</sup> Pearson, 1968, 7.

<sup>192</sup> Kevles, 1985, 202.

decision. He was aware that the Trust Committee was in favour of Haldane's appointment in November 1936.<sup>193</sup> It is therefore likely that he was influential on their decision. Watson also agreed to give the eugenics department half the money he had previously used for Haldane's salary if Haldane got the position. As the Rockefeller officer, W.E. Tisdale, wrote:

“Of the £600 which was liberated to W.'s [Watson's] Department by transferring H.'s [Haldane's] salary from that Department to the Weldon Bequest, £300 was bribe money to Fisher to permit H. [Haldane] to be appointed to the professorship in biometry.”<sup>194</sup>

In 1936 Watson was still heavily invested in Haldane. In November 1936 Watson spoke of the possibility that Haldane would be given the adjoining building to the DoZ. Watson informed the Rockefeller officer, H.M. Miller;

“he [Watson] would have to take over all details if this happened, as H. [Haldane] is quite incapable of dealing with ordinary business matters.”<sup>195</sup>

However, by June 1937 it had become clear that Haldane and his group would remain in the same building as the DoZ, although they would form their own department. Watson agreed to continue to provide animal quarters and servants for them.<sup>196</sup>

Watson also tried to arrange funding for Haldane's work. Haldane did not officially take up the position of Weldon professor until October 1937 and the finances were still being finalised in November 1937.<sup>197</sup> However, it must have been apparent at the end of 1936 that there would be little endowment to support the rest of Haldane's group. Watson therefore approached the Agricultural Research Council (ARC) for funding on Haldane's behalf.<sup>198</sup> He also negotiated

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<sup>193</sup> Miller's diary, November 16-17, 1936, RG 12.1, RFA.

<sup>194</sup> Tisdale's diary, November 29-30 and December 1, 1937, f579, b45, s401D, RG 1.1, RFA.

<sup>195</sup> Miller's diary, November 16-17, 1936, RG 12.1, RFA.

<sup>196</sup> Tisdale's diary, June 22-26, 1937, f579, b45, s401D, RG 1.1, RFA.

<sup>197</sup> Miller's diary, November 16-17, 1936, RG 12.1, RFA. Pearson, 1968, 7. Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL. Haldane to Miller, 19 November 1937, f579, b45, s401D, RG 1.1, RFA.

<sup>198</sup> Miller's diary, November 16-17, 1936, RG 12.1, RFA. Weaver's diary, February 7, 1938, f579, b45, s401D, RG 1.1, RFA.

funding for Haldane with the RF.<sup>199</sup> When the Foundation declined to fund Haldane until he had formulated a research proposal, Watson provided him with £200 to pay his researchers until the Foundation began funding the group again.<sup>200</sup>

Watson had not envisaged genetics as the major speciality in the Department. The focus of the 1931 application he made to the RF was comparative physiology,<sup>201</sup> although genetics was an important part of his 1927 plan.<sup>202</sup> However, the growth of genetics in his department was clearly compatible with the broader outline of his vision. It introduced an experimental approach towards problems of evolution and how animals function. When genetics in the Department was threatened Watson therefore stepped in to ensure that the group remained at UCL in close proximity to the Department.

In 1936/1937 institutional structures were put in place that assured the survival of genetics research at UCL, at least in the short-term.<sup>203</sup> Neither the necessary financial arrangements nor the necessary provision of accommodation to ensure this was permanent were put in place during my period of study. While the location survived, substantial changes in staff occurred at this time. This is discussed in the following section.

### **2.2.5 Changes in Staff and Research Priorities**

Throughout 1934/1935 the geneticists working at the DoZ remained those discussed above, with the loss of Koller in March 1935. In 1936/1937 the geneticists working in the department changed substantially. Lafon's year visit

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<sup>199</sup> See Miller's diary, November 16-17, 1936, RG 12.1, RFA. Tisdale's diary, June 22-26, 1937, f579, b45, s401D, RG 1.1, RFA. Tisdale's diary, November 29-30 and December 1, 1937, f579, b45, s401D, RG 1.1, RFA.

<sup>200</sup> Tisdale's diary, November 29-30 and December 1, 1937, f579, b45, s401D, RG 1.1, RFA. Weaver's diary, February 7, 1938, f579, b45, s401D, RG 1.1, RFA.

<sup>201</sup> In: Memorandum on the Present Condition of Zoological Studies and the Opportunities which Present Themselves for their Development at UCL, f589, b46, s401D, RFA, Watson outlines a plan whereby the other professor in the Department was a comparative physiologist.

<sup>202</sup> In: The Policy of the Zoological Department of UCL, 7 February 1927, f433, b30, s2, IEBA, Watson plans to employ both a professor of genetics and a professor of comparative physiology.

<sup>203</sup> As Haldane pointed out there was no guarantee that genetics would be researched there permanently. (Haldane to Miller, 19 November 1937, f579, b45, s401D, RG 1.1, RFA.)

ended before the start of 1936. Christie appears to have finished his PhD early in 1936.<sup>204</sup> Minns also seems to have finished his work in the department in 1936/37.<sup>205</sup> Gorer began working at the Lister Institute full-time in 1936.<sup>206</sup> In 1937 Gordon left the Department for a permanent lecturing job in Aberdeen.<sup>207</sup>

With the loss of these researchers, only Grüneberg and Philip were left of the original eight. However, new students entered the department. Helen Spurway and P.A.R. Street studied the population genetics of *Drosophila* from 1936 for their PhDs.<sup>208</sup> James Rendel joined the department in 1937.<sup>209</sup> In 1936 the Rockefeller Fellow, L. Csik, visited the laboratory part-time and worked on the differential effects of oxygen deprivation within a species.<sup>210</sup> With his departure, in 1937, came the arrival of Sara Bedichek, who worked on lethal genes and intersexes in *Drosophila* at the department in 1937/1938.<sup>211</sup>

The specific work of the department changed slightly due to the alterations in staff. However, the work remained academic. Research on serological and haemoglobin differences between strains of mice ended. The work on X-ray incited mutations and sexual preferences in *Drosophila* also appears to have been terminated. Grüneberg's work with mice had, by then, developed from a three point linkage test into research on the genetics of development. Philip's work on crossing over between the X and Y chromosomes had also changed into the investigation of population genetics with beetles and wild mice. Gordon's population genetics work with *Drosophila* was continued by Spurway, Street and

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<sup>204</sup> The last mention of Christie I have come across is in December 1935, although the work he was doing is mentioned as continuing in February 1936. (Grant in aid 35254, f578, b45, s401D, RG 1.1, RFA. Haldane to Tisdale, 15 February 1936, f579, b45, s401D, RG 1.1, RFA).

<sup>205</sup> The last mention of Minns I have found is in June 1936. (WET-WW, June 12, 1936, f579, b45, s401D, RG 1.1, RFA).

<sup>206</sup> Gorer is last mentioned in connection with UCL in December 1935. (Projects for Research in Animal Genetics, f578, b45, s401D, RG 1.1, RFA). His work is not mentioned by Haldane a letter he sent to Tisdale in February 1936 which outlined the group's work. (Haldane to Tisdale, 15 February 1936, f579, b45, s401D, RG 1.1, RFA). The last paper Gorer published stating his affiliation as UCL and the Lister Institute was published in 1937. (Gorer, 1937b).

<sup>207</sup> Miller's diary, April 12, 1937, RG 12.1, RFA. Tisdale's diary, f39, b3, s405D, RG 1.1, RFA.

<sup>208</sup> Gordon, Spurway and Street, 1939. Spurway to Collin, 26 July 1950, MS 20641: 84, Haldane papers, National Library of Scotland.

<sup>209</sup> First mention of Rendel is in Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL.

<sup>210</sup> Miller's diary, November 16-17, 1936, RG 12.1, RFA.

<sup>211</sup> Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL.

Rendel, although Street appears to have left the department in 1938.<sup>212</sup> Haldane worked on the linkage of human diseases.<sup>213</sup> Thus with the exception of Grüneberg and Haldane the research of the department was focused on population genetics by the end of 1937.

## 2.2.6 A Group Divided

The next major changes in the department occurred after the start of the Second World War, when the group became split. At the end of 1939, UCL evacuated to Wales, making no arrangements for the continuation of the DoB's work. Most of the DoZ were evacuated to Bangor.<sup>214</sup> This did not include the DoZ's cytologist, M.J.D. White, who was evacuated to the JI.<sup>215</sup> Thus, even without the formation of a separate department for the geneticists, they probably would not have been evacuated to Bangor. Philip moved with White to the JI due to the lack of available working space in the department.<sup>216</sup> This kept some contact between the two departments. However, the result was a physical separation of the DoB from the DoZ, which had not existed before because the two departments had shared the same building.

At the end of 1939 Haldane and Fisher both claimed that the College was obstructive towards the continuation of their research.<sup>217</sup> The feeling of being fellow victims seems to have brought the pair closer together. Haldane wrote to the RF:

“Professor Fisher and I have refused to quit...”<sup>218</sup>

“The College has continued in its attempts to eject Professor Fisher and myself...”<sup>219</sup>

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<sup>212</sup> The last mention I can find of Street in connection with the department is Haldane to Tisdale, 18 December 1937, b26, Haldane papers, UCL.

<sup>213</sup> Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL.

<sup>214</sup> Parrington and Westoll, 1974, 487.

<sup>215</sup> Miller to Weaver, 6 November 1939, f579, b45, s401D, RG 1.1, RFA.

<sup>216</sup> Miller to Weaver, 6 November 1939, f579, b45, s401D, RG 1.1, RFA.

<sup>217</sup> Haldane to Tisdale, 7 October 1939, f579, b45, s401D, RG 1.1, RFA. Fisher to O'Brien, October 4, 1939, Fisher (R.A.) papers.

<sup>218</sup> Haldane to “Sir”, 22 September 1939, f579, b45, s401D, RG 1.1, RFA.

<sup>219</sup> Haldane to Tisdale, 7 October 1939, f579, b45, s401D, RG 1.1, RFA.

Fisher also wrote to the Foundation:

“As Haldane has perhaps told you, I have been compelled to evacuate our former rooms in Gower Street, but have been fortunate enough to be accommodated here [at Rothamsted Experimental Station] by my former chief, Sir John Russell.”<sup>220</sup>

In October 1940 Haldane and the *Drosophila* geneticists (Spurway, Rendel, Hans Kalmus and Elizabeth Jermyn) all evacuated to Rothamsted too. Thus, the departments of biometry and eugenics both moved to the same physical location for the continuation of their research during the war. Whether this brought them closer together intellectually is unknown.

Two members of the DoB did not evacuate to Rothamsted in 1940. These were Philip, who moved to the JI as discussed above, and Grüneberg. At the end of 1939 most of the mouse colony was destroyed<sup>221</sup> and Grüneberg began to look for new accommodation.<sup>222</sup> In November 1939 he began to write a book on the genetics of the mouse at the Royal Cancer Hospital.<sup>223</sup> A year later, when the rest of the Department moved to Rothamsted, Grüneberg moved his work to the Mount Vernon Hospital, Northwood.<sup>224</sup> Some members of the department were therefore physically separated from the rest in 1939/1940. In Philip’s case this lasted until 1942 when she rejoined the group at Rothamsted.<sup>225</sup> While they were physically separated Haldane remained in contact with both Philip and Grüneberg and continued to offer advice about their work.<sup>226</sup>

While Philip and Grüneberg became physically separated from the rest of the Department, the other members, Spurway, Rendel, Kalmus<sup>227</sup> and Jermyn<sup>228</sup>,

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<sup>220</sup> Fisher to Miller, November 22, 1939, f221, b16, s401A, RG 1.1, RFA.

<sup>221</sup> Haldane to Sir, 22 September 1939, f579, b45, s401D, RG 1.1, RFA.

<sup>222</sup> Fell to Grüneberg, 3 October 1939, folder Fang-Firschberg, b5, Grüneberg papers.

<sup>223</sup> Kennaway to Grüneberg, 7 November 1939, folder Ken-Knu, b9, Grüneberg papers.

<sup>224</sup> Davies to Grüneberg, 2 October 1940, folder Roy (3), b14, Grüneberg papers.

<sup>225</sup> Haldane to Miller, 6 June 1942, f581, b45, s401D, RG 1.1, RFA.

<sup>226</sup> See for example, Haldane to Grüneberg, 7 March 1942, folder Hab-Hamilton, b7, Grüneberg papers.

<sup>227</sup> Hans Kalmus was a Czech refugee who joined the group in 1940. (Haldane to Weaver, 19 June 1940, b26, Haldane papers, UCL, Haldane to Huxley, 1 March 1940, b26, Haldane papers, UCL). He was supported by the Society for the Protection of Science and Learning. (Haldane to

became much closer. The group not only worked together at Rothamsted but they also all participated in physiology experiments for the Admiralty. The experiments required trust in each other since they were fairly dangerous. In one experiment Rendel was knocked unconscious and developed pneumothorax.<sup>229</sup> The accident, in 1940, made Rendel unfit for military service but by June 1942 he was well enough to do some light laboratory work.<sup>230</sup> As well as working together the group also lived together at Harpenden.<sup>231</sup>

In October 1942 Grüneberg joined the Royal Army Medical Corps<sup>232</sup> and Philip rejoined the group at Harpenden.<sup>233</sup> Following this all the active members of the DoB were located at Rothamsted. In 1943 Spurway was employed by the MRC to do full-time research for the Navy. At the same time, Haldane spent most of his time working for the Navy.<sup>234</sup> Thus by the middle of 1943 only Haldane, Rendel, Philip, Kalmus and Jermyn were actively engaged in research. By the time the war ended this group had dissolved. Until Grüneberg gained his release from the Army in 1946 only Haldane and Spurway were working in the DoB.<sup>235</sup>

### **2.2.7 The DoZ/B in Conclusion: An Exemplar of an Academic Location**

In section 2.2 I have outlined the history of genetics at the DoZ/B, UCL. I have shown that a group of geneticists came to work in the Department for a variety of reasons. One was Watson's vision of the Department; another was the RF's support of that vision. Equally important were the employment of Haldane and his vision of genetics at an academic location. Haldane was already working at a breeding location. His employment at an academic location allowed him to do a

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Weaver, 29 October 1940, b26, Haldane papers, UCL) He began work on the physiology of mutants (Haldane to Weaver, 19 June 1940, b26, Haldane papers, UCL), which later broadened to include their ecology. (Haldane to Miller, 9 July 1941, f580, b45, RG 1.1, RFA).

<sup>228</sup> Joan Elizabeth Jermyn was Haldane's secretary but she also began performing research at this time. (Haldane to Weaver, 29 October 1940, b26, Haldane papers, UCL).

<sup>229</sup> Haldane to Weaver, June 1940, b26, Haldane papers, UCL.

<sup>230</sup> Haldane to Miller, 3 June 1942, f581, b45, s401D, RG 1.1, RFA.

<sup>231</sup> Haldane to Weaver, 29 October 1940, f580, b45, s401D, RG 1.1, RFA.

<sup>232</sup> Grüneberg to Jacoby, 25 October 1951, folder Ja-Jac, b8, Grüneberg papers.

<sup>233</sup> Haldane to Miller, 6 June 1942, f581, b45, s401D, RG 1.1, RFA.

<sup>234</sup> Haldane to Hanson, 10 March 1943, f581, b45, s401D, RG 1.1, RFA.

<sup>235</sup> Haldane to Grüneberg, undated, folder Hab-Hamilton, b7, Grüneberg papers.

different type of genetics research. The RF's faith in Haldane and his vision of academic genetics was also vital.

Haldane's vision of academic genetics was experimental population genetics and physiological genetics. He saw academic research organisms as *Drosophila* and mice, although he indicated that he would like to use plants too.<sup>236</sup> This fitted Watson's vision of zoology because it included the experimental research of evolution and the function of animals. The questions that Haldane and his group tackled were therefore not just academic questions but broad questions with relevance to general zoological issues as well as the discipline of genetics itself. That this was true in practice and not just theory is shown by Watson's strong support for the work when it came under threat in 1936/1937.

Though the group focused more heavily on population genetics following the formation of a separate department, the work did not become any less broad in its applicability. This was probably both a function of Haldane's interests and the continuing presence of the group within the same building as the DoZ. Whether this changed when the group moved to Rothamsted is unknown since it is outside the period of this dissertation. It is an interesting question, however, since it would indicate the extent to which this breadth of application came from the geneticists themselves compared to the influence of their environment.

### **2.3 The IAG, Edinburgh**

In this section I discuss the history of the IAG at Edinburgh. This will provide the context for the analyses of the Institute's work that are provided in the next three chapters. It will also allow me to demonstrate that the Institute was within the breeding setting.

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<sup>236</sup> Haldane to Tisdale, 14 August 36, f579, b45, s401D, RG 1.1, RFA.



### 2.3.1 Forming an Animal Breeding Research Department

As is discussed in more detail below, in 1910 the British government set up a Development Commission (DC) to enhance rural life in Britain.<sup>237</sup> The Commissioners decided to establish, and support existing, agricultural research institutes with the money the Treasury had set aside for their work. Their plan was for each of the institutes to specialise in a particular aspect of agriculture, such as animal breeding.<sup>238</sup> The Commissioners appear to have been unsure, however, whether improving research in animal breeding was best achieved by establishing a new institute. They therefore appointed a committee under the direction of the geneticist, William Bateson, to advise them. The committee concluded that it was too early to concentrate such research at a single institute.<sup>239</sup> Nevertheless, in 1913 a Joint Committee was formed to establish and administer an Animal Breeding Research Department (ABRD) in Edinburgh on behalf of the DC.<sup>240</sup>

The Joint Committee was formed of representatives from the Board of Agriculture for Scotland, the East of Scotland Agricultural College and the UoE. This conjunction of interests was possibly brought about because the Commission could only consider proposals put forward by government departments.<sup>241</sup> The Board of Agriculture for Scotland submitted a proposal to the DC to fund animal breeding at the East of Scotland Agricultural College.<sup>242</sup> However, the UoE was also interested in hosting an animal breeding institute and had recently hired a farm to impress the Commissioners.<sup>243</sup>

However the Committee came about in 1913, it did not succeed in establishing an animal breeding institute until 1919. Histories of the institute tend to suggest that this was due to the First World War and the death of the geneticist, Arthur

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<sup>237</sup> Orwin and Whetman, 1964, 378.

<sup>238</sup> The bill and its implications are fully discussed in Olby, 1991a.

<sup>239</sup> Deacon, unpublished, 1. Olby, 1991a, 523.

<sup>240</sup> Ewing to Hutchison, 24 January 1927, folder Correspondence, IAGA.

<sup>241</sup> Olby, 1991a, 518.

<sup>242</sup> Olby, 1991a, 523.

<sup>243</sup> Olby, 1991a, 523.

Darbishire, who was expected to become director of the station.<sup>244</sup> Robert Olby has suggested that the delay may have been due to the Development Commissioners' unwillingness to establish an institute for animal breeding immediately. It was this, he claims, that led the Commissioners to only support the Joint Committee on a yearly basis until 1919.<sup>245</sup>

In 1919 the Joint Committee appointed the assistant in natural history at the UoE, F.A.E. Crew, as head of the ABRD.<sup>246</sup> For six months the department only existed on paper. As Crew put it:

“Nobody, including myself, had the foggiest notion concerning accommodation, staffing or research programme...”<sup>247</sup>

This situation did not last long. Crew toured Britain to see what problems needed researching. He visited the JI, universities, colleges, breeders and fanciers. He also visited T.H. Morgan's group at Columbia and learnt *Drosophila* techniques from them. On his return he found an old fever hospital that the university allowed him to take over for the department. He built his own furniture and animal pens, and collected animals to experiment with. These were mainly animals bred by fanciers such as mice, rats, guinea pigs, fowl and budgerigars, with the addition of *Drosophila*, rather than agricultural animals.<sup>248</sup> This was probably made necessary by the accommodation of the department. Crew recalled that he:

“trained the cocks to march down the steps into the cellar of the main building each night and back to their own pens next morning.”<sup>249</sup>

Thus by the end of 1920, a research institute with accommodation, research organisms and a Director, had been formed in Edinburgh to conduct research

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<sup>244</sup> McKeen, 2002, 2. Bulfield, 1999, 2. Crew, 1971, 291. The principal of UoE, J.A. Ewing, also gave the First World War as the reason for this delay. (Ewing to Hutchison, 24 January 1927, folder correspondence, IAGA).

<sup>245</sup> Olby, 1991a, 523.

<sup>246</sup> Crew, 1971, 291. Bulfield, 1999, 2. McKeen, 2002, 2.

<sup>247</sup> Crew, 1971, 292.

<sup>248</sup> Crew, 1971, 292. Deacon, unpublished, 4. Crew's autobiographical notes, folder autobiographical notes, IAGA. Hogben, 1974, 136-137.

<sup>249</sup> Crew, 1971, 292.

into the agricultural field of animal breeding. Crew, as Director, had begun to investigate the problems that an animal breeder should investigate and had started to acquire the necessary techniques with which to investigate them.

### 2.3.2 Joining the University

The Department grew quickly at the start of the 1920s. By 1924 it had outgrown the old fever hospital and moved into six rooms loaned to the Department by the Professor of Chemistry at the UoE, Sir James Walker.<sup>250</sup> The Department's accommodation in these rooms was only on a temporary basis. The Department was also facing financial difficulties. The institute was having difficulty raising the matching funds that were a condition of funding from the DC.<sup>251</sup> Crew therefore turned to the Agricultural Section of the IEB for aid at the start of 1925.<sup>252</sup> One of the results of the aid given by the IEB in 1926 was the Department's incorporation into the UoE.

The motivation for funding the Department's incorporation into the University appears to have been to ensure its permanence. As Robert Olby has shown, it was to ensure permanence that the DC originally set up new institutes in relation to a college or university.<sup>253</sup> When Crew approached the IEB he wrote:

“...this Department which though it has flourished exceedingly is threatened with extinction unless I can secure for it an endowment from some source other than Governmental.”<sup>254</sup>

The IEB tried to ensure the department's permanence in three ways. Firstly, it provided the university with enough funds for them to be able to build new accommodation for the department. Secondly, the Board provided funds towards the endowment of a Chair for Crew. This not only gave Crew a permanent position with full university status but it ensured that the Department was fully

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<sup>250</sup> Annual Report, 1924–1925, folder Annual Reports: 1924-1928, IAGA.

<sup>251</sup> A. R. Mann officer's diary, July 30, 1925, f569, b40, s2, IEBA.

<sup>252</sup> Crew to the Secretaries of the IEB, 24 March 1925, f569, b40, s2, IEBA.

<sup>253</sup> Olby, 1991a, 520.

<sup>254</sup> Crew to The Secretaries, 24 March 1925, f569, b40, s2, IEBA.

represented in the University Senate.<sup>255</sup> Thirdly, they made it a condition of the money that the university guaranteed an income for the department of £5,600 p.a.<sup>256</sup>

A condition of the grant was that all parts of the agreement had to be implemented. A.R. Mann of the IEB wrote to the principal of the UoE, Sir Alfred Ewing:

“It is further understood that the Board has considered the provision of endowment for the Chair, funds for the required building and facilities, and bringing the annual maintenance to the estimated basis, as all parts of one undertaking to establish this Department on a firm and permanent basis as an integral part of the University, and that the Board’s grants contemplate the realization of the entire program and are not to be considered independently without further action by the Board.”<sup>257</sup>

The IEB awarded the money to the UoE in 1926, but it required the university to find £26,000 towards the Chair’s endowment and building costs as well as guaranteeing the maintenance fund for the Department.<sup>258</sup> By June 1927 the University had received pledges from other sources that enabled them to meet all these conditions.<sup>259</sup> In 1928 the Joint Committee was wound up and the Animal Breeding Committee took its place. The new committee administrated the Department on behalf of the University. It advised the university court and submitted proposals to the court regarding the annual budget, staff appointments, research in progress and research that was being proposed.<sup>260</sup> As such the committee had influence over the research directed at the location, but the control lay in the hands of the university court. At the same time that the Animal Breeding Committee came into existence, Crew became the Buchanan Professor of Animal Genetics and the staff received lecturer status.<sup>261</sup> Building work began, and on 30 June 1930 the new buildings were officially opened as the

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<sup>255</sup> Mann to Rose, 30 March 1925, f570, b40, s2, IEBA.

<sup>256</sup> Mann to Ewing, June 9, 1926, f570, b40, s2, IEBA.

<sup>257</sup> Mann to Ewing, June 9, 1926, f570, b40, s2, IEBA.

<sup>258</sup> Mann to Ewing, June 9, 1926, f570, b40, s2, IEBA.

<sup>259</sup> CBA to Fleming, June 16, 1927, f571, b40, s2, IEBA.

<sup>260</sup> M1, folder Minutes, IAGA.

<sup>261</sup> M2, folder Minutes, IAGA. M3, folder Minutes, IAGA. Deacon, unpublished, 9.

‘Department of Animal Genetics’ at the UoE.<sup>262</sup> Plans of the building are given in Appendix Two.

### 2.3.3 Changing Scale

While negotiations with the IEB took place, additional changes occurred at the Department. When Sir James Walker lent the department rooms in 1924, he also provided them with access to seven acres of land.<sup>263</sup> Up to then the department’s work had been restricted to work on small mammals and birds.<sup>264</sup> By March 1927 the Department’s work included studies conducted on sheep, horses, cattle, pigs, goats, fowl, rabbits, rats, mice and *Drosophila*. In other words it had expanded to include research on agricultural animals. By 1927 the department had also gained access to another 28 acres of land.<sup>265</sup> The Department’s work thus became more recognisably agricultural in the time that the IEB negotiations occurred.

The ABRD also gained a library resource in 1929. Two years earlier a proposition had been made for an Imperial Information Bureau for animal breeding to be attached to the ABRD. The Bureau was to collect information about animal genetics, sex physiology and animal breeding from books, journals, correspondence and by sending out questionnaires. The information was then to be disseminated to the Colonies.<sup>266</sup> In 1929 such a Bureau, attached to the Department, was opened.<sup>267</sup>

Following the Department’s acquisition of its own accommodation in 1930 it grew considerably. At the end of 1928 there were six scientific members of staff, including Crew.<sup>268</sup> The work of the department was described by Crew as pure and applied research into animal breeding, the former being concerned with both

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<sup>262</sup> Yarcovich to Brierley, June 24, 1930, f571, b40, s2, IEBA.

<sup>263</sup> Annual Report, 1924–1925, Annual Reports: 1924–1928, IAGA.

<sup>264</sup> 3 December 1925. *The Wool Record and Textile World*. 19: 1659, folder Press Cuttings, IAGA.

<sup>265</sup> Annual Report, 1926–1927, folder Annual Reports: 1924–1928, IAGA.

<sup>266</sup> Crew to Fleming, 10 December 1928, folder Correspondence, IAGA.

<sup>267</sup> M4, folder Minutes, IAGA.

<sup>268</sup> M2, folder Minutes, IAGA.

genetics and sex physiology.<sup>269</sup> Two years later the Department employed fourteen scientific members of staff.<sup>270</sup>

Part of the expansion was in the breeding section of the department. In 1928 James Pickard was employed in the Department to do research on rabbit breeding. This was funded by the Ministry of Agriculture.<sup>271</sup> A major development in the animal breeding section of the department was the purchase of a farm in 1930.<sup>272</sup> A year later the Development Fund provided money for the accommodation of forty cows at the Institute.<sup>273</sup> The Department also received money to fund research into wool<sup>274</sup> and in 1929 the Department hosted a conference on wool breeding.<sup>275</sup>

The major part of the department's expansion was not in animal breeding, however, but in the area of sex physiology. In 1929 the President of Sun Life Insurance Company, T.B. Macaulay, gave one thousand shares in Insull Utility Investments, Inc. to the Department to fund the work of the endocrinologist, B.P. Wiesner.<sup>276</sup> A year later Macaulay gave the department eighty shares in the Capital Stock of the Sun Life Assurance Company of Canada. This paid for the appointment of three research assistants for Wiesner: P.G. Marshall, H. Taylor and J.M. Robson. Macaulay also gave money for the reconstruction of some buildings for the sex physiology section and guaranteed £3000 towards the section's maintenance for three years.<sup>277</sup> By May 1931, the section had acquired thousands of rats for their work,<sup>278</sup> including Wistar Rats.<sup>279</sup>

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<sup>269</sup> Annual Report, 1927–1928, folder Annual Reports: 1924-1928, IAGA.

<sup>270</sup> Annual Report, 1929–1930, folder IAG Annual Reports, IAGA.

<sup>271</sup> Interview with Crew, CD 7, IAGA.

<sup>272</sup> M7, folder Minutes, IAGA.

<sup>273</sup> M9, folder Minutes, IAGA.

<sup>274</sup> M7, folder Minutes, IAGA.

<sup>275</sup> 30 May 1929, *The Agriculturalist*, folder Press cuttings 4: March 1927 – July 1930, IAGA.

<sup>276</sup> M5a, folder Minutes, IAGA.

<sup>277</sup> M8, folder Minutes, IAGA.

<sup>278</sup> M10, folder Minutes, IAGA.

<sup>279</sup> Interview with Crew, CD 7, IAGA.

### 2.3.4 Refocusing

The guaranteed maintenance of the sex physiology section ended in 1932. At that time Britain was feeling the effects of the Great Depression. The shares Macaulay had given the Department were no longer producing any income and so the sex physiology section gradually disbanded. In June 1932 notice was given to three members of the sex physiology section. The group was kept functional by monthly payments from Macaulay<sup>280</sup> until 1934, when the university decided to terminate Wiesner's contract as they could no longer afford to employ him.<sup>281</sup> The last of the group, J.M. Robson, moved to the pharmacology department in 1935.<sup>282</sup> The one lasting effect of the sex physiology section was the maintenance of a Pregnancy Diagnosis Laboratory in the department.<sup>283</sup>

The IAG, as the ABRD was renamed in February 1931,<sup>284</sup> contracted in general during the early part of the 1930s. In 1932 the Development Commissioners withdrew £260 of support from the department, resulting in one member of the farm staff being made redundant.<sup>285</sup> The funding provided by the Empire Marketing Board to research the inheritance of wool ended in 1933, and so did I.W. Parnell's employment.<sup>286</sup> The ARC provided emergency aid to continue William Miller's research into this,<sup>287</sup> but Miller and the wool research moved to London at the start of 1935.<sup>288</sup> Thus, research on agricultural animals did not fare well in the first half of the 1930s.

In October 1932 the ARC inspected the Institute. Their report of the visit was not favourable. They concluded:

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<sup>280</sup> M12, folder Minutes, IAGA.

<sup>281</sup> M16, folder Minutes, IAGA.

<sup>282</sup> Anonymous to Sir Thomas, 10 October 1935, folder IAG, Annual Reports, IAGA.

<sup>283</sup> Anonymous to Sir Thomas, 10 October 1935, folder IAG, Annual Reports, IAGA.

<sup>284</sup> M9, folder Minutes, IAGA. No specific significance is attached to the renaming of the location. A shift towards more academic research did not occur until later in the decade. The name change presumably reflected the location's prior incorporation into the University of Edinburgh.

<sup>285</sup> M12, folder Minutes, IAGA.

<sup>286</sup> M13, folder Minutes, IAGA.

<sup>287</sup> M16, folder Minutes, IAGA. M17, folder Minutes, IAGA.

<sup>288</sup> M18, folder Minutes, IAGA.

“It is difficult to avoid the suspicion that the staff of the Institute does not contain sufficient men of real ability to direct so diverse a series of experiments as that which it has undertaken. The lack of a real statistician clearly leads to much wasted effort.”<sup>289</sup>

The committee recommended the employment of a cytologist as well as a statistician. The necessity for a statistician was in part addressed by the help given to the department by R.A. Fisher.<sup>290</sup> The need for a cytologist was addressed by the Institute in October 1933 when they employed the cytologist, P.C. Koller, on a series of impermanent grants.<sup>291</sup>

The ARC had taken over the DC's funding of the department in 1931. Following the visit, however, they threatened to withdraw their support of the department.<sup>292</sup> In 1933 the Burden Mental Disease Trust at Bristol offered the human geneticist, J.H. Fraser Roberts, a job and, in the financially insecure situation of the IAG at the time, he accepted.<sup>293</sup> In August 1934 Koller also decided that he could not remain in Edinburgh because of the financial situation. He therefore moved to London to work with Haldane while he found a more permanent job.<sup>294</sup> The pure genetics work of the department also suffered a degree of contraction during the 1930s.

While Edinburgh experienced a period of growth in the late 1920s, followed by a period of contraction in the early 1930s, the Institute that existed in 1935 was very different from that in 1924. Up to 1924 work was mainly conducted with small mammals and birds, as discussed in section 2.3.3. In 1935 research was being conducted as much with agricultural animals as non-agricultural animals.

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<sup>289</sup> A8, folder Memos, financial reports, IAGA.

<sup>290</sup> A8, folder Memos and Financial Reports, IAGA.

<sup>291</sup> M15, folder Minutes, IAGA.

<sup>292</sup> Miller's diary, April 28, 1933, RG 12.1, RFA shows that the ARC continued to assess the situation. It states that the ARC/DC ceased funding the department while it did so. This seems highly unlikely. The British Treasury agreed to contribute two thirds of the department's expenditure annually in 1926 (Ewing to Hutchison, 16 December 1926, f570, b40, s2, IEBA.) When asked if this had occurred in 1938 Crew stated that it had, except during the depression years when the sum dropped from the agreed £5600 to £5100 (Tisdale's diary, April 30, 1938, f44, b4, s405D, RG1.1, RFA).

<sup>293</sup> Miller's diary, April 28, 1933, RG12.1, RFA.

<sup>294</sup> Koller to Darlington, 14 August 1934, folder J.122, box c.110, Darlington papers.



There were also far more facilities for agricultural genetics than in the mid-1920s, since there was now a farm.

The dual character of the Institute's research was reinforced in May 1935 by the ARC. By then they had agreed to fund a reduced program of research at the Institute. The staff for this would be Crew as a geneticist, Koller would return from London as the cytologist, A.W. Greenwood as a physiologist, J.A. Fraser Roberts would return from Bristol to be their agricultural geneticist and A.D. Buchanan Smith as a livestock geneticist.<sup>295</sup> The number of people at the Institute was larger than this, however, due to the presence of students and guests.

### 2.3.5 Changing Focus

The continued agricultural function of the Institute into the late 1930s is shown by Crew's justification of the Institute's use of laboratory animals and study of pure genetics in the Annual Report for 1936-37.<sup>296</sup> However, in 1935 Crew began to try to shift the location's research away from agricultural genetics. An official departmental letter written in 1935 stated that the Institute would re-focus on cytogenetics. This was partly due to the lack of income that applied genetics was now generating compared to earlier in the 1930s (see sections 3.3.2.2, 3.3.2.3 and 3.3.2.5) and partly due to the cytogenetics section attracting more students.<sup>297</sup> Another reason for wanting the focus to shift away from agricultural genetics may have been that the farm was running to a deficit each year.<sup>298</sup> However, Greenwood was supplementing the location's income by supplying chickens to research institutes and individuals.<sup>299</sup>

The focus on cytogenetics wished for in 1935 was aided by the Institute's employment of the geneticist, H.J. Muller, in 1937/38.<sup>300</sup> A large team working

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<sup>295</sup> Weaver's diary, May 11, 1935, RG 12.1, RFA.

<sup>296</sup> Report and List of Publications for the year 1936-37, folder IAG Annual Reports, IAGA.

<sup>297</sup> Anonymous to Sir Thomas, 10 October 1935, folder IAG Annual Reports, IAGA.

<sup>298</sup> M22, folder Minutes, IAGA.

<sup>299</sup> Annual Report, 1936-37, folder IAG Annual Reports, IAGA.

<sup>300</sup> Muller worked at the Institute from November 1937, but he appears to have begun being paid at a slightly later date. (Crew to Sir, 17 February 1938, f44, b4, s405D, RG 1.1, RFA.)

on cytogenetic problems gathered around Muller almost immediately. By February 1938 he had two scientific assistants, two technical assistants and six postgraduate students, including Guido Pontecorvo.<sup>301</sup> Muller also collaborated with the cytologist already at the department, P.C. Koller.<sup>302</sup>

The Institute therefore changed its focus in the late 1930s towards pure genetics, which was more typical of an academic department. The impression of the Institute becoming more academic is reinforced by its instigation of the first BSc in genetics in Britain in 1939. The BSc was made a requirement for beginning a PhD at Edinburgh in order to raise the standard of PhDs produced.<sup>303</sup>

The international importance of the Institute is also indicated by its hosting of the Seventh International Genetical Congress in August 1939. This does not indicate its recognition as an academic location, however, since the Sixth International Congress of Genetics had been held at Ithaca, a breeding location, in 1932.<sup>304</sup>

### **2.3.6 A Dividing Location**

A number of changes occurred at the Institute following the start of the Second World War. Crew was called up for military service in 1939, leaving his deputy, A.W. Greenwood, in charge of the Institute.<sup>305</sup> Between 1938, when there were seventy five people at work in the Institute (including guests and technical staff),<sup>306</sup> and 1941 when there were thirty six people working there, the size of the Institute's staff halved.

In 1939 there was talk of the department having to give up its building for bacteriological work.<sup>307</sup> The war also caused problems obtaining supplies for the

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<sup>301</sup> Crew to Sir, 17 February 1938, f44, b4, s405D, RG 1.1, RFA.

<sup>302</sup> Memorandum H.J. Muller and Past fellow P. C. Koller, Edinburgh, October 28, 1938, f44, b4, s405D, RG1.1, RFA.

<sup>303</sup> Miller's diary, June 6, 1939, f45, b4, s405D, RFA.

<sup>304</sup> Jones, 1932.

<sup>305</sup> McKeen, 2002, 2.

<sup>306</sup> Interview with Crew, CD 8, IAGA.

<sup>307</sup> Koller to Darlington, 14 September 1939, folder J.131, box c.110, Darlington papers.

work of *Drosophila* geneticists,<sup>308</sup> and since funding became more difficult to obtain experiments had to be scaled back.<sup>309</sup>

In August 1940 Muller left the Institute to work in the United States.<sup>310</sup> He initially took unpaid leave for two consecutive years but in 1942 the University refused to grant him any more leave of absence and Muller's association with the Institute ended.<sup>311</sup> While Muller left the Institute, the cytogeneticists, Mr. and Mrs. Slizynski, found refuge there,<sup>312</sup> and in 1941 Charlotte Auerbach from the Institute and James Robson discovered that mustard gas had mutagenic effects.<sup>313</sup> Thus, while conditions at the Institute made work difficult, the focus of the work on cytogenetics problems appears not to have changed.

At the end of the Second World War Crew resigned as head of the IAG. He was replaced by the developmental geneticist, C.H. Waddington. By this time the ARC, upon whose funding the department was very much reliant, had decided to create a National Animal Breeding Research Organisation to consider the application of genetics to animal breeding. The genetics department at the Organisation, whose function would overlap with that of the IAG considerably, was to be headed by Waddington. Discussions between the various concerned bodies led to the decision that Waddington would take up the Buchanan Chair of Animal Genetics at Edinburgh and the Genetics Department of the National Animal Breeding Research Organisation would be housed at the Edinburgh Institute. The Institute itself became a normal university genetics department, also directed by Waddington.<sup>314</sup>

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<sup>308</sup> Koller to Demerec, 7 December 1939, folder Koller Peo C #1, Demerec papers.

<sup>309</sup> Koller to Demerec, 20 December 1939, folder Koller Peo C #1, Demerec papers.

<sup>310</sup> Carlson, 1981, 270-271. Koller to Darlington, 22 August 1940, folder J.133, box c.110, Darlington papers.

<sup>311</sup> Fleming to Muller, 24 March 1942, f47, b4, s405D, RG 1.1, RFA.

<sup>312</sup> Muller and Koller to Miller, 9 December 1939, f45, b4, s405D, RG 1.1, RFA.

<sup>313</sup> Beale, 1995, 27.

<sup>314</sup> Annual Report, 1945-46, folder IAG Annual Reports, IAGA.

### 2.3.7 A Breeding Location under Contention

From the history of the IAG we can see that it began as a breeding location for genetics. It was set up by the DC as part of their foundation of institutes to research science relevant to agriculture, horticulture and forestry. The ABRD's research was intended to aid agriculture.

During the 1920s the Department was incorporated into the UoE. However, its purpose did not change. Its work was still intended to aid agriculture not to increase understanding of a purely academic discipline. As an official Departmental publication stated in 1930:

“It may seem to some that as this Department has grown it has drawn further and further away from its original purpose, which was to provide the agriculturalist with accurate information concerning animal breeding. But this view would be both unjust and untrue.”<sup>315</sup>

Thus, the Department was not a hybrid location, despite being incorporated into a university, but was still clearly a breeding location.

During the 1930s the setting of the Institute came under growing contention. Koller's work on the cytogenetics of meiosis could be interpreted as increasing understanding of breeding and thus of benefit to agriculturalists. However, Muller's work on mutagenesis was clearly directed towards increasing understanding of an academic discipline: cytology.<sup>316</sup> I still would not classify the department as a hybrid location because the dual nature of the research was not intended for a purpose. I believe that Crew needed the money provided by the ARC and thus the Institute remained focused towards agriculture. However, I think he wanted it to be more academic. In 1940, Koller wrote that Crew had told him:

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<sup>315</sup> A7, folder Memos, financial reports, IAGA.

<sup>316</sup> Details of this work are provided in Chapter Five (section 5.4.2)

“he would like to stop the A.R.C. grant, and to turn the Institute into a pure University Department.”<sup>317</sup>

The contention as to which setting the Institute belonged ended in 1945, when the site of the Institute came to house a breeding location for genetics (the genetics department of the National Animal Breeding Research Organisation) and an academic location (the genetics department of the UoE). The institute therefore split along the lines of setting. The positioning of both locations in the same place was purposeful. Though the two were discrete entities, and should be considered as such, if they were considered together there would be a case for this entity being a hybrid location. This would be interesting in itself, since a hybrid location would have arisen from a location under contention. This, however, is speculative and outside the scope of my study.

## **2.4 An Institutional History of British Genetics**

In this section I discuss how the relative importance of the different settings for genetics research changed in Britain between 1900 and 1940. This gives the context in which the DoZ/B and the IAG were established and run. Knowing their context will enable me to consider how representative they were of genetics locations within their respective settings (academic and breeding). The discussion also examines my first thesis: that genetics grew at different rates in different settings in 1930s Britain. This thesis is important because it means that knowledge of the effects setting had on scientific research is necessary for understanding genetics in 1930s Britain.

### **2.4.1 Methodology**

#### **2.4.1.1 Defining a Geneticist**

The definition of a geneticist is a historical concept and will, therefore, have changed over time. In Britain, major steps towards defining genetics as a discipline occurred in 1910 when the *Journal of Genetics* was established, and in

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<sup>317</sup> Koller to Darlington, 16 September 1940, folder J.133, box c.110, Darlington papers.

1919 when the Genetical Society was founded. The former helped to define what genetical research was; the latter helped to define who was a geneticist. In the 1930s a British geneticist would ideally be defined as someone who worked in Britain, published in the *Journal* and attended the Genetical Society because these indicate that they worked in Britain, were actively engaged in research and were members of the genetics community.

Though the above definition is theoretically sound, there are methodological problems attached to it. The first is that the Genetical Society membership lists only exist for 1933, 1934 and 1936-1939. Anyone who worked in Britain at the start of the decade and then migrated, retired or died may therefore be missed. This problem can partly be solved by using attendance at the Seventh International Genetical Congress in 1939 as another indication of membership of the genetical community. Doing so reveals another potential problem. Researchers who published in the *Journal of Genetics* and attended the Seventh International Genetical Congress were far less likely to be members of the Genetical Society if they lived in Scotland. This is due to the Congress being held in Scotland and the Genetical Society meetings being held in the South of England. Geographical considerations could therefore bias the population considered to be geneticists when membership of societies are considered.

The above is, however, only of minor concern. More difficult is the problem that in this section I wish to compare growth of genetics in Britain. A consistent definition is therefore required. The Genetical Society membership lists for the 1920s no longer exist, and the International Genetical Conferences were not held in Britain, as the one in 1939 was. Who a geneticist was therefore has to rely on publication in the *Journal of Genetics* for the 1910s and 1920s. For the 1910s, 1920s and 1930s I have therefore defined a British geneticist as someone who worked in Britain and published in the *Journal of Genetics* more than once in the decade. This excludes researchers who did not work in Britain and those who did not consistently research genetics in the decade. As appendix three shows, during the 1930s about 70% of the geneticists thus defined attended the Seventh International Genetical Congress and about 70% were members of the Genetical

Society. The population I have called geneticists was therefore a relatively unified scientific community during the 1930s.

The first decade of the 1900s presents more of a problem, as the *Journal* can no longer be used to indicate who the geneticists were. I have not therefore tried to present an analytical assessment of who a geneticist was during that decade. Instead, I have relied upon the secondary literature to provide a historical context for the discussion of geneticists in future decades.

Below I identify genetic locations between 1900 and 1940. These were the geographic sites where a cohesive group of geneticists or an individual geneticist (as hereby defined) performed research. They have been classified into settings by the purpose of the location, and not by the research conducted. The only exception to this is in the case of amateurs, where there was no other information available. This means that the distinction between the settings would exist even if they differed in no other respect. As I show in Chapters Three to Five, they also differed in funding, organism use and problem choice.

#### 2.4.1.2 Defining Genetics

The term, ‘genetics’, refers to the science of heredity. As the practices and theory of genetics has changed over time, the meaning of the term will also have changed. I have therefore attempted to identify which aspects of genetics were considered as important and unimportant to its identity during the 1930s, to distinguish genetics from related subjects.

The Mendelian theory of inheritance appears to have been a crucial part of genetics identity. The following quotes are taken from a number of different books published during the 1930s:

“THE science of genetics ... may be said to have received its first systematic basis on the general recognition of Mendel’s generalisations...”<sup>318</sup>

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<sup>318</sup> Sansome and Philp, 1932, v.

“It was by experiments with garden crops again that Mendel laid the foundations of the science of genetics, which deals with the heredity principle invoked by Darwin in his evolutionary theories...”<sup>319</sup>

“FEW biologists will doubt that heredity, the subject matter of genetics is one of the important problems of biology. Indeed, when Mendel’s results were rediscovered in 1900 and the new science of genetics got under way, it appeared to some authors that a new era was dawning in biological thought.”<sup>320</sup>

What were deemed far less important were the methods of genetics:

“...an overemphasis on technique nearly always obscures the real interest of a science, which lies in the concepts and theories to which the experimental methods open the door.”<sup>321</sup>

Crew wrote as early as 1927:

“It is reasonable to hold that in all probability the present methods of genetics, so ably used, have already made their great and lasting contributions to biological science.”<sup>322</sup>

As such genetics was not about technique, but neither was it about ultimate ends. As seen in Chapter Five the geneticists in the academic setting tended to reach out to other disciplines for their problems. Geneticists in the breeding setting worked to improve breeding.

During the 1930s genetics was neither a set of methods, nor an end. Instead, it was a body of theory relating to the structure, transmission, action and evolution of genes. Any research that investigated genes, for whatever end and by whatever method is therefore taken in this thesis as genetics research.

This definition means that genetics research cannot be counterpoised to breeding research. As Crew pointed out during the 1920s, genetics was one of the

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<sup>319</sup> Crane and Lawrence, 1934, vii.

<sup>320</sup> Waddington, 1939, 7.

<sup>321</sup> Waddington, 1939, 7.

<sup>322</sup> Crew, 1927, vii.



breeding sciences.<sup>323</sup> Similarly, the secretary of the Medical Research Council, Walter Fletcher, argued while the Agricultural Research Council was being established, the council should deal with the agricultural sciences not agricultural science.<sup>324</sup>

#### **2.4.2 1900-1910: The Emergence of Settings for Genetics in Britain**

In the first decade of the Twentieth Century academic, breeding and medical settings for genetics all formed in Britain. The largest setting prior to 1910 was the academic setting.

The major advocate of genetics in Britain was William Bateson, who was employed as the deputy to the professor of zoology and comparative anatomy at Cambridge University from 1899.<sup>325</sup> He collaborated in his research with the Newnham College, Cambridge University, botany lecturer, Miss E.R. Saunders.<sup>326</sup> Their research was supported by the Evolutionary Committee of the Royal Society,<sup>327</sup> to whom they argued their research was the first step in understanding the origin of species.<sup>328</sup> A number of students from the university, especially from Newnham College, helped Bateson and Saunders with their research, often becoming independent. A number of Newnham employees also began to conduct genetics experiments. For example, the physiology lecturer, Florence Durham, studied the inheritance of coat colour in mice and the research fellow, Muriel Wheldale, investigated the inheritance of flower colour in snapdragons.<sup>329</sup> R.C. Punnett, who was a demonstrator in the Department of Zoology, also joined the research group, originally aiming to look at sex determination<sup>330</sup> but later looking at factors such as linkage.<sup>331</sup>

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<sup>323</sup> Crew, 1925, x.

<sup>324</sup> DeJager, 1993, 136.

<sup>325</sup> Richmond, 2001, 65.

<sup>326</sup> Crew, 1969, 9. The role of women at Newnham College, Cambridge, in researching genetics, 1900-1910, is discussed by Richmond, 2001.

<sup>327</sup> Kevles, 1980, 449-450.

<sup>328</sup> Bateson, (William), and Saunders, 1902, 3.

<sup>329</sup> Richmond, 2001, 69.

<sup>330</sup> Richmond, 2001, 70-71.

<sup>331</sup> Bateson, (William), Saunders and Punnett, 1908, 2-3.

During the first decade of the Twentieth Century thirteen Cambridge researchers were closely associated with Bateson.<sup>332</sup> They came together at the Cambridge Botanical Gardens, where Bateson rented an allotment for genetics research.<sup>333</sup> This then was the first major academic location for genetics research in Britain. Genetics research was conducted in the academic setting elsewhere however. L. Doncaster moved from Cambridge to the University of Birmingham around 1907, where he continued to research how the Mendelian ratios arose.<sup>334</sup> A.H. Trow, of the University College of South Wales, investigated the genetics of groundsel in the hope it would shed light on evolutionary relationships from around 1906.<sup>335</sup>

While the academic setting dominated genetics prior to 1910, some genetics research was done at a site that would form a genetics location in the breeding setting during the 1920s. Rowland Biffen, who worked in the School of Agriculture, Cambridge, performed breeding experiments with wheat for the purpose of:

“raising improved varieties from the point of view of the farmer and miller, and also to ascertain to what extent Mendel’s Laws of Inheritance hold for the distinctive characteristics of wheat.”<sup>336</sup>

Amateurs also studied genetics in Britain. One such was Redcliffe Salaman who worked at his home in Barley, Hertfordshire to improve potato crops from 1906.<sup>337</sup> His home was thus a breeding location.

Some research also occurred in Britain that was directed towards increasing understanding of disease. The physician, Archibald Garrod, investigated the

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<sup>332</sup> Richmond, 2001, 56.

<sup>333</sup> Bateson, (Beatrice), 1928, 1-150. William Bateson appears to have originally paid for use of the allotment but to have used it rent-free during 1901-1905 (Bateson (William), and Saunders, 1902, 3; Bateson, (William), Saunders and Punnett, 1905, 4).

<sup>334</sup> Bateson (William) papers.

<sup>335</sup> Trow, 1912-1913a, 239-240.

<sup>336</sup> Engledow, 1950-1951, 13.

<sup>337</sup> Salaman, 1910-1911, 7.

effect of inbreeding on the incidence of diseases such as alkaptonuria, albinism, cystinuria and pentosuria.<sup>338</sup>

Genetics research occurred in all of the three settings identified in Chapter One (section 1.3). It mainly occurred in the academic setting, with some work occurring in the breeding and medical settings.

### **2.4.3 1910-1920: The Basis for Growth in the Breeding Setting**

The greatest change in the British genetics settings during the 1910s was the growth of the breeding setting. This occurred in both locations dedicated to horticulture and locations dedicated to agriculture. The first horticultural breeding location arose following the death of the philanthropist, John Innes, in 1904. In his Will, Innes made a bequest for the establishment of a school of horticulture. As Innes' Will underwent probate it was agreed by the Board of Agriculture, the Charity Commissioners and the Trustees of the Will that the function of the horticultural institution would be research. In 1910 William Bateson became Director and Plant Breeder of the JI. Plant breeding was one, though not the only, area of research at the Institution. Mycology, entomology and biochemistry were also studied there. Nevertheless, the JI became one of the most important breeding locations for genetics in Britain in 1910.<sup>339</sup> It was the second largest location during the 1910s, employing four geneticists. (See appendix four).

Two other breeding locations employed geneticists during the 1910s. The first was Kew Gardens, where the Assistant Director studied the domestication of *Primula*.<sup>340</sup> The second was the South East Agricultural College at Wye. Research was done there on crossing hops<sup>341</sup> and the hybridisation of flax.<sup>342</sup>

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<sup>338</sup> Hopkins, 1936-1938, 225, 227-228. For details of Bateson's co-operation with physicians see Olby, 1991b. A medical professor, Dr. Carter, at the university of Birmingham also expressed interest in genetics. (Doncaster to Bateson, 13 March, Bateson (William) papers).

<sup>339</sup> An account of the establishment of the JI is given in Olby, 1989.

<sup>340</sup> Hill, 1912. Hill, 1917/18.

<sup>341</sup> Salmon, 1913-1914.

<sup>342</sup> Eyre and Smith (G.), 1915-1916.

Wye had been in existence since 1894<sup>343</sup> and it is unknown whether genetics research was performed there prior to 1910.

Other developments also occurred during the 1910s that would later lead to the enlargement of the setting in Britain. In 1910 a Development Commission (DC) was established by the British Government. The Commission was created to encourage the regeneration of rural Britain.<sup>344</sup> The Commissioners decided that the best way to achieve this was to encourage and rationalise agricultural research. Among other agricultural research institutes, they established a Plant Breeding Institute at the School of Agriculture, Cambridge University, in 1912, a Welsh Plant Breeding Station in Aberystwyth in 1919, an ABRD in Edinburgh in 1919/1920 and a Scottish Plant Breeding Station just outside Edinburgh in 1921.<sup>345</sup>

Rowland Biffen was appointed director of the Plant Breeding Institute at Cambridge, where he continued his research on the genetics of breeding wheat. This developed into a breeding location, employing a geneticist in the strict sense, during the 1920s. The Welsh Plant Breeding Station focused on improving grasslands. The director of the Station, George Stapledon, took an ecological approach to this but during the 1920s other members of staff, such as T.J. Jenkins, were geneticists. The history of the ABRD has been discussed in detail above. The Scottish Plant Breeding Station was mainly concerned with sorting varieties of potatoes rather than the genetics of breeding. However, geneticists, such as J.W. Gregor, were employed there during the 1920s. For further details of this research see the section below on the 1920s. During the 1910s and early 1920s the DC helped to establish four future breeding locations for genetics.

The academic setting grew slightly in terms of the number of locations it had during the 1910s and remained the largest setting for genetics in Britain, employing over half the British geneticists. In 1908 a chair of biology was created at Cambridge University. One of the conditions of the endowment was

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<sup>343</sup> Brassley, 1995, 469.

<sup>344</sup> A detailed discussion of the political context for the Commission and the institutes it set up is given by Olby, 1991a. See also Palladino, 2002, chapter two and Orwin and Whetman, 1964.

<sup>345</sup> Cooke, 1981, 10-12.

that the occupier would teach and research genetics. The Chair was held by Bateson until 1910 and Punnett subsequently. In 1912 it was made permanent and its name was changed to the Arthur Balfour Chair of Genetics.<sup>346</sup> Punnett was joined at the location by P.C. Bailey, who collaborated with him to research the genetics of fowl and rabbits. Bailey was killed, however, during the First World War.<sup>347</sup> Thus the academic location at Cambridge gained stability during the 1910s through the action of the university. It remained the largest location for genetics in Britain, with ten researchers during the decade.

The next largest location was the University of Reading. Frederick Keeble and C. Pellew investigated the genetics and chemistry of flower colour there in the early 1910s. Keeble moved to Wisley Gardens in 1914, however, and undertook other work.<sup>348</sup> C. Pellew moved to the JI prior to then, where she continued genetic research.<sup>349</sup> Genetics research was also performed at Reading by W.N. Jones.

Geneticists were also employed at a number of other academic locations during the 1910s. A.H. Trow continued to work at the University College of South Wales.<sup>350</sup> J.W.H. Harrison was employed at Armstrong College, Newcastle University.<sup>351</sup> R.R. Gates worked at Imperial College, Bedford College and Kings College, London.<sup>352</sup> J.B.S. Haldane was a Fellow at Oxford University. Research was also performed by H. Drinkwater at the University of Edinburgh and C. Dobell at Imperial College. The University of Birmingham was lost as an academic location, as Doncaster moved back to Cambridge University.

The medical setting also maintained its small size during the 1910s. In 1912 Garrod became a full physician and did not have time for experiments any more.<sup>353</sup> However, R.R. Gates was employed for a time at St. Thomas' Hospital.<sup>354</sup>

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<sup>346</sup> Bateson, (Beatrice), 1928, 123.

<sup>347</sup> Crew, 1967, 316-317.

<sup>348</sup> Blackman, 1952-1953, 492-493.

<sup>349</sup> Pellew, 1913/1914.

<sup>350</sup> See for example, Trow, 1912-1913b.

<sup>351</sup> Peacock, 1968, 245.

<sup>352</sup> Fraser Roberts, 1964, 87-88.

<sup>353</sup> Hopkins, 1936-1938, 225, 228.

<sup>354</sup> Fraser Roberts, 1964, 87.

#### 2.4.4 1920-1930: The Growth of the Breeding Setting

The 1920s saw a large growth of the breeding setting. The major focus of genetics research became the JI, which employed thirteen geneticists during the decade, over twice as many as the next largest location in Britain. In 1926 the JI's director and an icon of British genetics, William Bateson, died. He was replaced by A.D. Hall, a past director of Wye agricultural college and Rothamsted Experimental Station. Hall had been one of the Development Commissioners and had also been on the Board of Agriculture.<sup>355</sup> Though a very experienced breeder, Hall was not a geneticist. He therefore appointed the mathematical population geneticist, J.B.S. Haldane, as genetics adviser.<sup>356</sup>

Three of the other locations in the breeding setting were established by the Development Commission, which was founded in 1910 as discussed above. The ABRD was discussed above. The Plant Breeding Institute at Cambridge, part of the School of Agriculture, employed F.L. Engledow, who investigated the genetics of barley and wheat,<sup>357</sup> and A.E. Watkins, who investigated the genetics and cytology of wheat.<sup>358</sup> The Welsh Plant Breeding Station employed T.J. Jenkin during the decade, who investigated the genetics of ryegrass.<sup>359</sup>

While the locations mentioned above were the most important in the breeding setting, a new location emerged at the Department of Agriculture, University College of North Wales in Bangor, where J.A. Fraser Roberts studied the genetics of sheep.<sup>360</sup> Another new location was Wisley Gardens, where B.H. Buxton researched the biochemical genetics of flower colour.<sup>361</sup>

Thus, the breeding setting for genetics research continued to grow throughout the 1920s. During the 1910s the academic setting had been the largest in Britain,

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<sup>355</sup> Orwin and Whetman, 1964, 376-377. Olby, 1991a, 523.

<sup>356</sup> Lawrence, 1962, 5.

<sup>357</sup> Engledow, 1923 and Engledow, 1924.

<sup>358</sup> See for example, Watkins, 1924.

<sup>359</sup> See for example, Jenkin, 1926-1927.

<sup>360</sup> See for example, Fraser Roberts, 1924.

<sup>361</sup> Buxton and Darbishire, 1929.

during the 1920s the breeding setting was the largest, employing roughly half the British geneticists.

The academic setting for genetics decreased slightly in number of researchers during the 1920s. This was mainly due to the loss of researchers at the University of Cambridge. This remained the second largest location in Britain, but was about half the size it was in the 1910s. This was possibly because Punnett encouraged no other researchers. Following a visit in 1927, the American geneticist, L.C. Dunn, wrote that there was an “absence of active encouragement of graduate study in genetics. I suspect Punnett is responsible for this...”<sup>362</sup>

The University College of South Wales and Monmouthshire remained an active genetics location in the academic setting during the 1920s, although Trow was replaced by W.B. Crow.<sup>363</sup> Gates continued work at Kings College, London and Harrison at Armstrong College, Newcastle University. The academic location at Oxford University enlarged during the decade. Haldane was still based there at the start of the decade. Julian Huxley worked on rate genes there during the 1920s<sup>364</sup> and R. Snow worked in the botany department.

Less important individuals in the academic setting included Ruth Bamber and E. Catherine Herdman, who began researching the genetics of coat-colour in cats at the University of Liverpool during the 1920s.<sup>365</sup> At Leeds University, F.W. Dry investigated the genetics of coat-colours.<sup>366</sup> Trinity College, Dublin and UCL also employed a geneticist each in the form of F.W.R. Brambell and A.S. Parkes respectively.

The medical setting remained very small throughout the 1920s. Research was done by P.J. Cammidge and H.A.H. Howard in London on the genetics of hyperglycaemia in mice,<sup>367</sup> but neither were geneticists as defined above.

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<sup>362</sup> Dunn to Hutchison, January 26, 1928, folder Hutchison, C.B. (white folder), Dunn papers.

<sup>363</sup> See for example, Crow (W.B.), 1924.

<sup>364</sup> Baker, 1976, 220-221.

<sup>365</sup> See for example, Bamber and Herdman, 1927.

<sup>366</sup> Dry, 1924 and Dry, 1925-1926, Dry, 1928-1929.

<sup>367</sup> Cammidge and Howard, 1925-1926.

#### 2.4.5 1930-1940: The Growth of the Medical Setting

Genetics in 1930s Britain was characterised by a growth in numbers in the medical setting. Four locations formed in this setting, all of which employed influential geneticists. The first location arose at the Department of Eugenics, UCL, in 1932. In 1932 the biometrician, Karl Pearson, retired as head of the Galton Laboratory. The College decided to split the Laboratory into two: the department of eugenics, led by the population geneticist, R.A. Fisher, and the department of statistics, led by the statistician, Egon Pearson. Karl Pearson had not accepted the Mendelian laws and so genetics had never been a feature of the Galton Laboratory's work. However, with the succession of Fisher geneticists were employed at the eugenics department. For example, Kenneth Mather researched the linkage of genes.<sup>368</sup>

Another medical location for genetics was the Royal Eastern Counties' Institution. In 1930 Edmund O. Lewis, a physician and one of the trustees of the Darwin Trust, proposed a joint venture by the Trust, the MRC and the Royal Eastern Counties' Institution to research the causes of mental illness. In 1931 Lionel Penrose was appointed to the post, where he researched the inheritance of mental diseases.<sup>369</sup>

The Department of Social Biology at the London School of Economics also formed medical genetics location at the start of the 1930s. In 1930 Hogben was employed at the London School of Economics as Professor of Social Biology. The final medical location was the Burden Mental Research Department in Bristol. In 1933 the geneticist, John Fraser Roberts, was appointed principal investigator and worked on the genetics of intelligence there.<sup>370</sup>

The breeding setting continued to grow during the 1930s, such that about two thirds of British geneticists were employed in the setting during the decade. The two most important locations in the setting were the JI and the IAG, Edinburgh.

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<sup>368</sup> Lewis, 1992, 25.

<sup>369</sup> Kevles, 1985, 150-151, 156.

<sup>370</sup> Polani, 1992, 309, 313.



Both enlarged their capacity to support geneticists, despite both undergoing a difficult decade. The JI suffered financial loss with the Great Depression and appears to have lost staff as a result of this in 1932.<sup>371</sup> Nevertheless, the Institute employed approximately a third of the British geneticists during the decade. The Institute also underwent changes of leadership and organisation. In 1937 J.B.S. Haldane resigned from the JI to become full-time professor of biometry at UCL. He was replaced by Kenneth Mather, who had been working at the Galton Laboratory with Fisher. In the same year the Institute was divided into four departments: Genetics, Cytology, Pomology and Biochemistry,<sup>372</sup> led by Mather, Cyril Darlington, M.B. Crane and J.R. Price respectively.<sup>373</sup> In 1939 Sir Daniel Hall retired as head of the Institute and was replaced by Darlington.<sup>374</sup> The reputation of the JI remained high, as shown by H.J. Muller's consideration of the director's job in 1938.<sup>375</sup>

The IAG<sup>376</sup> also went through a turbulent decade during the 1930s, as described above. Briefly, it lost a large number of its scientific staff between 1932 and 1935, when the depression caused the Institute to lose a portion of its income and the ARC reconsidered its funding of the department. The Institute refocused its efforts away from sex physiology and agricultural genetics onto cytogenetics. This probably accounts for its increased employment of geneticists.

The three Plant Breeding Institutes founded by the DC were all active locations for genetics research during the decade. At the Welsh Plant Breeding Station Jenkin continued his research into the genetics of grass,<sup>377</sup> R.D. Williams and R.A. Silow researched the genetics of clover<sup>378</sup> and W. Ellison researched the cytogenetics of the herb, *Avena*.<sup>379</sup> The Agricultural School at Cambridge University also remained an active location. In 1931 Biffen retired<sup>380</sup> and was

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<sup>371</sup> Lawrence, 1980, 33. Lewis, 1983, 120.

<sup>372</sup> Lewis, 1983, 121.

<sup>373</sup> JI Annual Report 1937, f449, b35, s401D, RG 1.1, RFA.

<sup>374</sup> Lewis, 1983, 121.

<sup>375</sup> H.M. Miller officer's diary, June 22, 1937, RG 12.1, RFA.

<sup>376</sup> The ABRD officially changed its name to the IAG in 1931.

<sup>377</sup> See for example, Jenkin, 1935.

<sup>378</sup> See for example, Williams and Silow, 1933 and Williams, 1938-1939b.

<sup>379</sup> See for example, Ellison, 1937.

<sup>380</sup> Engledow, 1950-51, 11.

replaced by Herbert Hunter, who did not believe that genetics was important to plant breeding.<sup>381</sup> However, A.E. Watkins and H.W. Howard researched the genetics of wheat<sup>382</sup> and swedes<sup>383</sup> respectively during the 1930s. S. Ellerton and L.E. Morris also investigated genetics there during the decade. The least active of the Plant Breeding Stations was the Scottish one, although research was done into the genetics of potatoes by W. Black<sup>384</sup> and the geneticist, J.W. Gregor researched the genetics of wild plants.

Growth in the breeding setting during the 1930s also occurred in horticultural locations. At Kew Gardens E.M. Marsden-Jones and W.B. Turrill undertook a variety of genetics investigations.<sup>385</sup> Wisley Gardens also appears to have been a site of some genetics research. B.H. Buxton thanked the gardens for their help in his paper of 1931/1932.<sup>386</sup>

Fraser Roberts continued working at the British Research Association for the Woollen and Worsted Industries in Leeds until 1931, when he joined the IAG.<sup>387</sup> Research was also performed by geneticists employed at the University College of North Wales, Jealott's Hill Research Station and Rothamsted.

The academic setting retained the size it was during the 1910s, but continued to decline in comparison to the other settings. The two major locations were the Department of Zoology/Biometry at UCL and the Department of Botany at Kings College, London. In 1932 the DoZ at UCL employed Haldane as a part-time professor of genetics. Following his employment at UCL, a number of other geneticists were subsequently employed to work at the department and in 1937 they gained their own department. These developments were discussed in detail above. This location (the DoZ/B), along with the JI and the IAG was one of the major locations for genetics research in 1930s Britain.

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<sup>381</sup> Palladino, 2002, 45-46.

<sup>382</sup> See for example, Watkins and Cory, 1931-1932.

<sup>383</sup> See for example, Howard, 1938.

<sup>384</sup> See for example, Black, 1933.

<sup>385</sup> See for example, Marsden-Jones and Turrill, 1934.

<sup>386</sup> Buxton, 1931/1932.

<sup>387</sup> Polani, 1992, 309.

The other major academic location was the Department of Botany at Kings College, London. R.R. Gates had worked here since 1919 but he was joined by the geneticist, D.G. Catcheside in 1931.<sup>388</sup> S. Ramanujam and G.S. Bhatia also worked at the location during the decade.

Punnett retained his Chair at Cambridge University during the 1930s.<sup>389</sup> Catcheside<sup>390</sup> and R. Scott-Moncrieff<sup>391</sup> were also employed at the University during the decade, but worked in the botany and biochemistry departments respectively, rather than with Punnett. Liverpool University also remained an academic genetics location, as Bamber and Herdman continued to work there.<sup>392</sup>

New academic locations for genetics arose during the 1930s at Manchester and Aberdeen. F.W. Sansome was employed at Manchester University to work on the genetics of plants from 1936.<sup>393</sup> Sansome was accompanied by his wife, E.R. Sansome, who studied cytogenetics.<sup>394</sup> Aberdeen University employed L. Hogben as head of the Natural History Department, and C. Gordon to research population genetics.<sup>395</sup>

Genetics locations also existed at Glasgow University, Exeter University and Eton College during the decade. At the former, Catcheside did research before moving to Kings College.<sup>396</sup> M.M. Richardson and L.E. Morris performed research at the other locations respectively, although Morris moved to the School of Agriculture at Cambridge at the end of the decade.

The academic setting therefore did not grow in terms of number of locations or with respect to the other settings, but it grew by about 50% in terms of number of researchers due to the emergence of the DoZ/B as a major location for genetics research.

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<sup>388</sup> Fincham and John, 1995, 122.

<sup>389</sup> Crew, 1967, 318.

<sup>390</sup> Fincham and John, 1995, 123.

<sup>391</sup> See for example, Scott-Moncrieff, 1931-1932.

<sup>392</sup> See for example, Bamber and Herdman, 1932.

<sup>393</sup> Miller's diary, January 31, 1936, RG 12.1, RFA.

<sup>394</sup> Sansome (E.R.), 1938.

<sup>395</sup> Tisdale's diary, June 27-28, 1937, f39, b3, s405D, RG 1.1, RFA.

<sup>396</sup> Fincham and John, 1995, 121-122.

The 1930s was therefore a time of great growth in British genetics. This occurred dramatically in the medical and breeding setting; it also occurred in terms of numbers of researchers in the academic setting.

#### **2.4.6 Thesis One: During the 1930s British genetics expanded unevenly across the different ‘settings’ in which it was studied.**

In the above sections (2.4.2-2.4.5) I have demonstrated the growth of genetics in Britain during the 1930s. I have categorised the locations where this research occurred into three settings, the breeding, academic and medical settings. In section 2.4.5 I have shown that the medical setting expanded the number of locations it had for genetics study from none to four during the decade. The number of researchers increased from none to five in the same period. The breeding setting doubled in terms of researchers, from twenty four to fifty six. The number of locations it had also roughly doubled, from six to eleven. The academic setting also saw growth in terms of researchers of about 50% during the decade, but not in terms of the number of locations that existed for it.

Bearing the above findings in mind, understanding the changing nature of genetics in 1930s Britain requires knowledge of the different contexts the settings provided for genetics research. In this dissertation I investigate the breeding and academic settings, as these were the largest two during the 1930s. An investigation of the medical setting is clearly required, however, since it was the quickest growing setting during the decade.

### **2.5 How Representative the DoZ/B and the IAG were of their Respective Settings**

In this section, I consider how representative the DoZ/B and the IAG were of academic and breeding locations for genetics in the 1930s. This will build on the descriptions given in sections 2.2 and 2.3 to consider how applicable my findings are to the academic and breeding settings in general.

### 2.5.1 The DoZ as an Academic Location

The Department had considerable similarities to other academic locations. One similarity was its age. The DoZ/B came into existence as a genetic location during the 1930s. Of the nine academic locations that existed in the 1930s, six had not previously existed. Only the Department of Genetics at Cambridge appears to be unusual in this respect, dating back to 1912.

Another similarity was the employment of only one geneticist by the College. Though the department at UCL had more geneticists than other academic locations, only Haldane's employment was guaranteed by the university. Though four geneticists existed at Kings College, only two were employed there and at Cambridge the three geneticists worked in separate departments. It was therefore typical to employ one or two geneticists and for others to occasionally work with those geneticists. The number of geneticists UCL employed at the location was thus typical, even though it appears otherwise due to the presence of other geneticists on temporary grants.

The presence of these extra geneticists points towards the location developing in a slightly unusual manner. This was due to a number of contingencies, such as Haldane being attractive to the RF, his willingness to take refugees and having the working space to allow this. It was not due to the location being atypical of the academic setting *per se*.

This slightly unusual development led to the transformation of the location in 1937, when the geneticists gained their own department. At that time the geneticists became the only researchers in the location.<sup>397</sup> This slightly unusual feature should not be overemphasised. The department remained in the same building as the DoZ. In terms of daily work routine nothing changed.

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<sup>397</sup> The only other academic location where this was true is the Department of Genetics at Cambridge. The locations at Newcastle and Manchester were botany departments, the location at Oxford was a department of zoology, the location at Aberdeen a natural history department and that at Cambridge a biochemistry department. The departments at Liverpool and Imperial College are unknown.

The DoZ/B had many features in common with other academic locations in the 1930s: it was young, only one geneticist was guaranteed employment and it directed its work towards increasing the understanding of an academic discipline. The disciplines varied between zoology, botany, genetics and biochemistry. Zoology was the most common such discipline, followed closely by botany. The location developed in a slightly unusual manner, however, resulting in a large number of genetics researchers working there and the acquisition of a department for those geneticists.

### **2.5.2 The IAG as a Breeding Location**

The IAG was, in my view, more typical of its setting than the DoZ/B on formation. The IAG, the JI, the Plant Breeding Institute, the Welsh Plant Breeding Station, the Scottish Plant Breeding Station, Kew Gardens and Rothamsted Experimental Station all had connections to the DC. All of these, with the exception of the JI, Kew and Rothamsted, were set up and supported by the Commission.<sup>398</sup> The Commission supported plant pathology at Kew Gardens; and plant nutrition and soil problems research at Rothamsted.<sup>399</sup> The Commissioners planned to fund plant breeding research at the JI but there is no evidence to suggest that they actually did so.<sup>400</sup> No links are known between the Commission and Wisley Gardens, the British Research Association for the Woollen and Worsted Industries or to private individuals.

Another similarity between most of the breeding institutes was the links they had to universities. The ABRD was jointly run by the East of Scotland Agricultural College and UoE. In 1928 it became an integral part of the university itself. The Plant Breeding Institute was set up as part of the Agricultural Faculty of Cambridge University. It was therefore integral parts of the university from their inception.<sup>401</sup> The Welsh Plant Breeding Station was linked to the Agricultural

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<sup>398</sup> Olby, 1991a, 522-523. Palladino, 2002, 43-44. Cooke, 1981, 15.

<sup>399</sup> Brassley, 1995, 475-476.

<sup>400</sup> Olby, 1991a, 522.

<sup>401</sup> Palladino, 2002, 43.

Department of the University College of Wales.<sup>402</sup> The JI also had academic ties. Members of its research staff were recognised as teachers by the University of London. Such staff could supervise students studying for postdoctoral degrees awarded by the University of London.<sup>403</sup> The Scottish Plant Breeding Station did not have links to a university.<sup>404</sup> No university links are known for Kew Gardens, Wisley Gardens, Rothamsted or the British Research Association for the Woollen and Worsted Industries.

The major differences between the locations came from their defined research function. The IAG was unusual because it exclusively studied the genetics of animals. Among other breeding locations, this was only true at the British Research Association for the Woollen and Worsted Industries. The majority of the locations exclusively studied plants. This was true of the Plant Breeding Institute, the Welsh Plant Breeding Station, the Scottish Plant Breeding Station, Kew Gardens, Wisley Gardens, Jealott's Hill Research Station and Rothamsted. The JI studied both plants and animals but focused on the genetics of plants.<sup>405</sup> The research functions of the locations varied from animal breeding, plant breeding, sheep breeding, horticultural research and soil studies.

This comparison of the breeding locations for genetics in 1930s Britain shows that the IAG was fairly typical of breeding locations in Britain. The main difference between it and other locations was in its focus on animals rather than plants.

## 2.6 Conclusion

Genetics locations can be categorised into breeding, academic and medical settings during the 1930s. The breeding setting was the largest setting during the decade, and doubled in terms of both locations and researchers. The academic setting grew in terms of the number of researchers working within the setting

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<sup>402</sup> Palladino, 2002, 50-51.

<sup>403</sup> The JI, f449, b35, s401D, RG 1.1, RFA.

<sup>404</sup> Palladino, 2002, 48.

<sup>405</sup> The JI, 1910-1935, f449, b35, s401D, RG 1.1, RFA.

during the decade but not in terms of the number of locations. The fastest-growing setting was the medical setting. This grew many times over both in terms of locations and researchers.

British genetics changed greatly in character throughout the 1930s. The three settings I have identified also experienced differential growth during the decade. This means that a full understanding of the change in British genetics during the decade cannot be gained without taking the concept of setting into consideration. My dissertation provides an analysis of the type of genetics found in the academic and breeding settings. My findings can therefore be used to begin to explain the changes seen in genetics during the decade. The explanation cannot be complete, however, until similar research has been done on the medical setting.

The DoZ/B and the IAG were two of the most important genetics locations in 1930s Britain. Though both showed some slightly unusual features for locations in their respective settings, both provide reasonable exemplars of academic and breeding locations respectively. In the following chapters I investigate different characteristics of science at each location to see how they differed. I then investigate whether the defining characteristics of science identified for each location were typical of their setting.



## Chapter Three

### Funding

#### 3.1 Introduction

This Chapter is the first of three investigating the defining characteristics of genetics in different settings in 1930s Britain. In this Chapter I focus on funding. I establish what differences existed between the funding bodies that supported genetics at the DoZ/B and the IAG, the type of support they offered and the likelihood of these differences being representative of those between the academic and breeding settings.

I begin, in section 3.2, by comparing the relationships that existed between the two locations and a mutual funding body, the Rockefeller Foundation (RF). I show that the Natural Sciences Division (NS) of the RF favoured academic genetics activities. This led to its funding being concentrated in the academic setting, though it did not recognise the boundaries between settings. I show that the RF favoured certain organisational structures and encouraged their formation in the groups it supported. The RF influenced British genetics by promoting academic genetics and by encouraging long-term research directed towards a question of wide applicability.

In section 3.3 I compare the bodies that supported genetics at the two locations and the type of support they offered. Finally, in section 3.4, I survey the funding bodies that supported other British genetics locations, to investigate whether the differences in funding seen between the locations were representative of differences across the two settings. In these sections I show that there was very limited alternative funding to that offered by the RF for genetics in the academic setting. This usually resulted in geneticists working in physical isolation from each other in the setting. The DoZ/B shows another possible outcome, which was the growth of an unstable group. Locations in the breeding setting were maintained by funding from the Development Commission (DC)/ Agricultural Research Council (ARC). This gave the Bodies considerable control over the

permanent staff employed at locations in the breeding setting. However, funding was also available from many other bodies to support specific projects. This meant that locations in the breeding setting could take on a wide variety of shapes, depending upon the project-focused funding they sought.

## **3.2 The Rockefeller Foundation**

In this section I investigate the changing relationships the DoZ/B and the IAG had with the RF. This shows that the NS of the RF was prepared to fund genetics in the academic and breeding settings, but only if the activities were academic. The following sections also show that the Foundation was individual and programme focused in its funding. It funded highly-regarded scientists to work on long-term programmes of research.

### **3.2.1 Background to the Foundation's Support of Genetics in the 1930s**

The Rockefeller philanthropies began to fund science in 1923. At that time, Wickliffe Rose took control of the General Education Board (GEB) on the condition that it would fund natural and agricultural science world-wide. However, the charter of the GEB restricted its operation to the United States and re-negotiating it may have threatened the Board's existence.<sup>406</sup> Philanthropies were not very popular in America at the time. They were seen as elitist and threatening to democracy. The current view was that no-one had voted for the philanthropies and so they had no mandate by which to influence public life to the extent they did.<sup>407</sup> As I show later, this heavily influenced the RF's policies during the 1930s, as it tried to maintain a benign appearance. In the 1920s, John Rockefeller Junior, who wanted Rose to run the GEB, avoided renegotiating the GEB's charter by creating the International Education Board (IEB) to fund scientific research and training globally.<sup>408</sup> Since the Boards were intended to support education, the science they were interested in supporting tended to be university based, though not necessarily academic in activity.

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<sup>406</sup> Kohler, 1991a, 135.

<sup>407</sup> Karl and Katz, 1987.

<sup>408</sup> Kohler, 1991a, 135.

At the end of 1928 the Rockefeller philanthropies were reorganised to consolidate them and prevent their functions overlapping. The International Health Board, the GEB and the IEB were incorporated into the RF, as was the social sciences work of the Laura Spelman Rockefeller Memorial. The Foundation reorganised into five Divisions: Natural Sciences, Medical Sciences, International Health, Social Sciences and Humanities.<sup>409</sup> The former two took over the task of funding genetics research in America and abroad. The Medical Sciences Division funded medical genetics activities, and the Natural Sciences Division funded academic genetics activities. Agricultural genetics activities were not funded by the RF. Since activity type tended to correlate with the type of setting, the Natural Sciences Division (NS) is the main focus of my attention.

Though the Foundation took over areas of interest from various Rockefeller philanthropies, the divisions reformulated their aims. The NS was slower to do this than other divisions because it had five different directors between 1928 and 1932.<sup>410</sup> However, there were some policy changes in that time. One part of natural science that was explicitly excluded from the funding programme was agricultural research. In September 1931 the Rockefeller official, L.W. Jones, wrote to Crew:

“No doubt you are aware of the fact that the IEB, at the close of the year 1928, ceased to operate as a Board undertaking new ventures in fields of Science and of Agriculture. It is true, as you know, that, during the active existence of the IEB, problems in Agriculture and in Animal Breeding were pursued with great vigour and great interest, and many projects were financed in these fields. However, at the time of the re-organisation, when the program of the IEB was taken over by the RF, it was particularly in Agriculture, Animal Breeding and related fields that drastic limitations were placed upon the projects which might be undertaken.”<sup>411</sup>

In February 1932 Warren Weaver became the director of the NS. Throughout 1932 and 1933 he developed a funding policy for the Division through a process of negotiation with the Trustees. Weaver’s background was applied mathematics.

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<sup>409</sup> Kohler, 1991a, 239.

<sup>410</sup> Kohler, 1991a, 245.

<sup>411</sup> Jones to Crew, September 4, 1931, f44, b4, s405D, RG1.1, RFA.

His expertise was therefore in the physical sciences, which the IEB had previously supported. However, the RF was traditionally a biomedical philanthropy, and the Trustees favoured funding biomedical sciences to funding physical sciences. Weaver was able to combine the two by developing a funding programme that supported research into vital processes using any promising scientific approach, including physical science approaches. Weaver was not very specific about what he meant by vital processes, but he seems to have had an experimental approach to biological questions in mind. One specific area that was mentioned at the end of 1933 was genetics.<sup>412</sup> By this Weaver meant academic genetics activities, since they were intended to investigate vital processes.

In the following sections I demonstrate that while the RF recognised the difference between academic and breeding genetics activities, it did not recognise a difference between academic and breeding genetics settings. Just as Weaver did not accept that biology could only be researched by biologists, the Division did not accept that academic genetics could only be researched by geneticists in the academic setting. I show that the Division was prepared to support any programme of research into academic genetics questions that was led by a scientist who had their full confidence, regardless of the setting in which they worked.

I demonstrate that the RF had six main concerns when considering genetics funding proposals: whether the proposed work was academic in its activity (the specifics were not important), the confidence they had in the main funding recipient, the stability of the main recipient's position, whether the recipient had formulated a long-term programme of research, the value it was likely to get for its money and whether another funding body was likely to take over funding the research. These conditions were designed to ensure that the work would increase understanding of vital processes and that the Foundation would get good value for money. The Foundation's programme had a long-term aim and so its funding

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<sup>412</sup> Kohler, 1991a, 269-283.

was not short-sighted. As well as funding established scientists, the RF funded the training of promising young geneticists.

### **3.2.2 The RF and the DoZ/B**

In this section I study the RF's interaction with geneticists working at an academic location. I demonstrate that within the academic setting the RF was not concerned with the content of the work conducted. Its main concerns were the excellence of the main recipient and the stability of their position. The RF considered both of great importance for enabling a programme of research to be developed at the location that would provide significant results about vital processes.

#### **3.2.2.1 Developing a Relationship**

When Haldane became professor of genetics at UCL he was aware of the RF as a potential source of funding from its support of the biological sciences' integration at Cambridge University during the 1920s.<sup>413</sup> His job had also been created by the RF's provision of funding for the DoZ and so he knew the Foundation was invested in the success of Watson's vision. However, Haldane had not received funding from the RF. In this section I investigate the process by which the Foundation judged Haldane worthy of its support. This demonstrates the value it placed on the stability and quality of a researcher and its interest in academic genetics activities.

It seems unlikely that the RF saw Haldane as a potential recipient of their funding in 1933. The reports regarding his work were favourable<sup>414</sup> but the Foundation preferred to fund individuals in stable situations. In 1932/33 Haldane was expecting to be appointed to the directorship of the John Innes Horticultural Institution (JI). As Weaver recorded in his diary:

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<sup>413</sup> Kohler, 1991a, 184.

<sup>414</sup> Dunn to Hutchison, January 26, 1928, folder Hutchison, C.B. [white folder], Dunn papers.

“H.[aldane] again indicates, quite frankly, his expectation to succeed Sir Daniel Hall at John Innes...”<sup>415</sup>

However, the RF maintained contact with Haldane. This was possibly because Haldane had previously supervised Rockefeller Fellows<sup>416</sup> and was therefore seen as a potential supervisor for them in future. The Foundation valued his opinion of other scientists.<sup>417</sup> It also knew that not everyone thought Haldane would succeed Sir Daniel Hall to the directorship of the JI.<sup>418</sup>

In March 1934 Haldane told a Rockefeller officer that he planned to remain at UCL on his succession to the directorship of the JI.<sup>419</sup> Having discovered that Haldane’s situation was more stable than previously thought, the Foundation began to investigate the possibility of funding his work at UCL. They began by gathering information on Haldane’s quality as a researcher. This helped to determine the extent of the support they were prepared to offer. In 1934 the American geneticists, T.H. Morgan and C.C. Little, independently told Weaver that Haldane was a promising geneticist.<sup>420</sup> At the end of 1934 the European officer, W.E. Tisdale, also wrote to Weaver:

“J.B.S. Haldane and R.A. Fisher are the only two geneticists with real possibilities in Europe today. NS must eventually enter into genetics activities with these two scientists.”<sup>421</sup>

The information the NS collected on Haldane shows that it wanted to support scientists who conducted high quality work. It also shows, however, that they were dependent upon American scientists for identifying such people.

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<sup>415</sup> Weaver’s diary, November 30, 1932, RG 12.1, RFA.

<sup>416</sup> Such as M. Graubard in 1933 (Miller’s diary, April 25, 1933, RG 12.1, RFA) and Wilcox in 1934 (Miller’s diary, March 8, 1934, RG 12.1, RFA).

<sup>417</sup> Haldane gave his opinion of Fritz Schiff, Julia Bell, Sjogren, Kenneth Mather, D. Zulueta, Dorothy Wrinch, Elton, C. H. Waddington and J. Needham to H.M. Miller in March 1934. (Miller’s diary, March 14-15, 1934, RG 12.1, RFA).

<sup>418</sup> Weaver’s diary, October 25, 1932, RG 12.1, RFA.

<sup>419</sup> Miller’s diary, March 14-15, 1934, RG 12.1, RFA.

<sup>420</sup> Weaver’s diary, April 24, 1934, RG 12.1, RFA. Weaver’s diary, August 20, 1934, RG 12.1, RFA.

<sup>421</sup> WET to WW, November 17, 1934, f578, b45, s401D, RG1.1, RFA.

During 1934 the Foundation decided Haldane was worthy of their support. His work was of a high quality and his position reasonably stable. Its interest in Haldane also demonstrates the RF's interest in academic rather than breeding genetics activities. The Foundation was interested in supporting his work at UCL but not at the JI. This was in spite of his position at the JI appearing to be more stable.

### 3.2.2.2 One-year grants

During the 1930s the RF made four awards to Haldane, to support his work over a five year period. In this section I investigate the first three of these grants, all of which were for a single year. This discussion demonstrates that while the RF valued stability it would make exceptions. It was prepared to invest in top-quality researchers to assure their employment at a location that allowed them to undertake academic genetics activities. While doing so, however, the RF used its influence to encourage the researcher to form a long-term programme of research. This encouraged the type of organisation and broadly applicable research the RF favoured.

As the RF became interested in funding Haldane in 1934, his need to obtain soft-money to support his research group also grew. In 1933/1934 a group of geneticists built up around him on temporary grants. In March 1934 there were four geneticists: Grüneberg, Philip, Gorer and Gordon. Grüneberg and Philip had two-year grants, as discussed below. Gorer was supported by his father.<sup>422</sup> Gordon had a grant from a South African source.<sup>423</sup> By October 1934 Koller had joined the group. He had no income. His living expenses were paid by Haldane and the cytologist, Cyril Darlington.<sup>424</sup> Gordon's grant was also due to end in December 1934.<sup>425</sup> Haldane wanted to retain both Koller and Gordon. This was probably so he could focus on population genetics work, as discussed in Chapter Two (section 2.2.3). By the end of 1934 Haldane therefore required funding to

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<sup>422</sup> Miller's diary, March 14-15, 1934, RG 12.1, RFA.

<sup>423</sup> Haldane to Miller, November 3, 1934, f578, b45, s401D, RG1.1, RFA.

<sup>424</sup> Miller's diary, October 22, 1934, RG 12.1, RFA. Haldane to Miller, November 3, 1934, f578, b45, s401D, RG1.1, RFA.

<sup>425</sup> Haldane to Miller, November 3, 1934, f578, b45, s401D, RG1.1, RFA.

retain Koller and Gordon so he could instigate his vision of population genetics at the location. The RF's willingness to fund the DoZ/B and the DoZ/B's need to be funded therefore converged at the end of 1934.

Haldane was very cautious in approaching the Foundation for aid at that time. The Foundation's officer, H.M. Miller, recorded in his diary: "he still states emphatically that he does not want much money..."<sup>426</sup> In the letter he sent the Foundation stating his needs Haldane did not write how much money he required, just which items of equipment and which salaries.<sup>427</sup> The RF was more interested in funding visions than every-day research. However, in this case the RF funded Haldane for a single year. This was presumably because approval of a grant for several years required a programme of research to be presented to the Trustees. This took some time to develop but Haldane required funding quickly to retain Gordon and Koller to be able to instigate his vision. Funding was approved by the Trustees for one year from February 1935.<sup>428</sup>

In May 1935 Tisdale visited Haldane at UCL again. Haldane was once again facing financial difficulties as Grüneberg's and Philip's funding from the Central British Fund for German Jewry was due to expire in July. There was little prospect of such difficulties going away due to the way the group had built up at UCL. Tisdale and Weaver agreed that it would be beneficial to provide Haldane with a capital sum.<sup>429</sup> Though Tisdale did not record the reasons for this, the Foundation preferred to support scientists over a period of years. This enabled the recipients to tackle problems with wide applicability, and thereby forward the Rockefeller's plan of investigating vital processes. The RF not interested in funding work that was only of relevance to genetics itself.

At the start of October 1935, Haldane's concerns about supporting Grüneberg and Philip led him to ask the Foundation for financial assistance for another year.<sup>430</sup> Tisdale visited Haldane a few weeks later. Haldane was once again

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<sup>426</sup> Miller's diary, October 22, 1934, RG 12.1, RFA.

<sup>427</sup> Summary of work in Progress October 3, 1934, f578, b45, s401D, RG1.1, RFA.

<sup>428</sup> Research Aid Grant, NS Paris R.A.Action No.4, f578, b45, series 401D, RG1.1, RFA.

<sup>429</sup> Tisdale's diary, May 16, 1935, f578, b45, s401D, RG1.1, RFA.

<sup>430</sup> Tisdale to Weaver, October 3, 1935, f578, b45, s401D, RG1.1, RFA.



cautious. Tisdale recorded: "H.[aldane] insists that he wants no splurge..."<sup>431</sup> In line with his and Weaver's previous discussions, Tisdale encouraged Haldane to produce a two to three year programme of research.<sup>432</sup> Tisdale did not tell Haldane the Division wanted to fund his work for several years, however, presumably in case the proposal was rejected by the RF's Trustees.

Haldane presented his proposed programme of work to the Foundation in December 1935. On receiving it, Tisdale decided to grant Haldane funding for one year while he discussed the proposal with Haldane and the Provost of UCL, Allen Mawer.<sup>433</sup> These discussions confirmed that both the JI and UCL were happy for Haldane to remain at UCL if he became director the JI, and thus that it was feasible for Haldane to undertake a long-term programme of work at UCL. Tisdale's discussions with Mawer were also designed to encourage UCL to allocate a fixed amount of money to Haldane's section.<sup>434</sup> This enabled the Rockefeller to calculate how much money Haldane's programme required from them and to make its funding conditional upon UCL providing the group with a certain level of support. These were standard terms for Rockefeller grants. It ensured the researcher had enough money to complete their research without having to turn to the Foundation for further aid.

During these discussions in March 1936 the director of the JI, Sir Daniel Hall, told Tisdale that the arrangements for his successor would be made circa June 1936. To confirm the situation was as it appeared, Tisdale waited until then before pushing forward the proposal.<sup>435</sup> In June/July Haldane found out that he was not going to be appointed director of the JI. As a result he began looking for employment in the United States.<sup>436</sup> By November the possibility of Haldane being appointed Weldon professor at UCL had arisen, as had possible support

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<sup>431</sup> Tisdale's diary, October 21 and 22, 1935, f578, b45, s401D, RG1.1, RFA.

<sup>432</sup> Tisdale's diary, October 21 and 22, 1935, f578, b45, s401D, RG1.1, RFA.

<sup>433</sup> Tisdale to Weaver, December 17, 1935, f578, b45, s401D, RG1.1, RFA. It was not unusual for the Foundation to fund the work of a potentially large funding recipient while the project was being finalised. Abir-Am has shown this occurring in the case of Needham and Waddington at Cambridge during the 1930s. (Abir-Am, 1988).

<sup>434</sup> Tisdale's diary, March 9 to 11, 1936, f579, b45, s401D, RG1.1, RFA.

<sup>435</sup> Tisdale's diary, June 12, 1936, f579, b45, s401D, RG1.1, RFA.

<sup>436</sup> Miller's diary, July 9-10, 1936, RG 12.1, RFA.

from the ARC.<sup>437</sup> With the situation still uncertain, Tisdale decided to make another yearly grant to Haldane.<sup>438</sup>

### 3.2.2.3 Watson and Haldane seek long-term support

Until 1937 Haldane had cautiously asked the Rockefeller for funding to keep his group afloat in the immediate future. The RF pushed Haldane to develop a long-term research programme at UCL but would only fund him annually because his situation was unstable. During 1937 the RF's stance towards Haldane changed. It refused to fund him annually any more and demanded a research programme if their funding relationship was to continue. This change of approach reveals that while the RF was prepared to fund on a contingent basis to assure the future of genetics in a location that allowed academic genetics activities to occur, it needed to be assured that progress towards working on an academic research programme was being made.

In June 1937 Tisdale told Haldane and Watson, who was then trying to assure the future of Haldane's group at UCL,<sup>439</sup> that the Rockefeller had only been supporting Haldane on an annual basis until his position was assured, as it now was. He said the Division would, however, consider funding any programme put forward.<sup>440</sup> Despite this, in November 1937, Haldane wrote to Miller that he hoped the Foundation would still provide money as in the past. He wrote that he would put forward a more ambitious scheme if desired.<sup>441</sup> Haldane had therefore still not made the transition to seeing the RF as a body that would assure the long-term future of his group.

In May 1937 Tisdale and Weaver had agreed that they wanted to support Haldane for an extended period beginning in 1938.<sup>442</sup> They were not prepared to continue supporting his work on a temporary basis. The RF officers therefore

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<sup>437</sup> Miller's diary, November 16-17, 1936, RG 12.1, RFA.

<sup>438</sup> Tisdale to Weaver, December 17, 1936, f579, b45, s401D, RG1.1, RFA.

<sup>439</sup> As discussed in Chapter Two (section 2.2.4).

<sup>440</sup> Tisdale's diary, June 22-26, 1937, f579, b45, s401D, RG1.1, RFA.

<sup>441</sup> Haldane to Miller, 19 November 1937, f579, b45, s401D, RG1.1, RFA.

<sup>442</sup> Weaver to Tisdale, May 13, 1937, f579, b45, s401D, RG1.1, RFA. Tisdale to Weaver, June 18, 1937, f579, b45, s401D, RG1.1, RFA.

appear to have reached a position where they felt they could no longer justify short-term grants to the Trustees. The Trustees wanted to see return on their investment, in this case an investment that Haldane would make the transition to a long-term, programme-based form of research.

Though Tisdale had told Watson and Haldane in June 1937 that the Foundation would only fund a long-term programme in future, he was concerned to see in November/December 1937 that no arrangements had been made to provide for Haldane's group when the current Rockefeller grant ended. Tisdale expressed his concern to Watson and told him that the Rockefeller could not press the matter.<sup>443</sup> The Rockefeller therefore began to make use of Watson's entry into its relationship with Haldane. The RF knew that Watson had money which he could make immediately available to Haldane. Having discussed the matter with Watson, Tisdale again told Haldane that the Foundation would be prepared to study any long-term research program he put forward.<sup>444</sup>

It became apparent to both parties at the end of 1937 that the relationship between the Rockefeller and Haldane's research group had turned into one of dependence. Haldane wrote Tisdale an emotive letter asking for advanced warning if the Rockefeller was not going to fund him any more so he could give his staff notice.<sup>445</sup> Tisdale, as already noted, expressed his concern regarding this to Watson. The RF tried to avoid creating dependence situations by involving the university or another funding body from the start. This is discussed further below. This was important to the image the RF wished to portray of itself as a benign funding body. Refusing funding to a dependent client made the RF look bad, while continuing to fund them meant it lost control of its own grants. However, Haldane's group's dependence on RF funding gave the RF a lot of leverage. At the end of 1937 it refused to renew Haldane's funding unless he provided the NS with a research programme to fund. Since Haldane required the RF's funding, he had no choice but to formulate a research programme for his group.

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<sup>443</sup> Tisdale's diary, November 29-30 and December 1, 1937, f579, b45, s401D, RG1.1, RFA.

<sup>444</sup> Tisdale's diary, November 29-30 and December 1, 1937, f579, b45, s401D, RG1.1, RFA.

<sup>445</sup> Haldane to Tisdale, 26 November 1937, b26, Haldane papers, UCL.

### 3.2.2.4 Developing a Program of Research

In this section I investigate the process of creating a programme of research. I show that the Foundation had a strong vision of what a research programme looked like and imposed this upon Haldane. The form of the programme imposed a structure of work and group organisation. This, in itself, placed some restriction upon the content of the research. However, the RF was careful to appear as not placing any restrictions upon research content.

Days after Tisdale's visit in November/December 1937, Haldane sent him a letter stating what research was currently occurring and what personnel he would like to add to the department.<sup>446</sup> Tisdale replied asking Haldane to state what his programme of research was. Tisdale tried to make his meaning clear by giving examples of other researchers' programmes. He wrote:

“...my group will want to know what your program of research in genetics is to be. ... A suggestion of the kind of thing I will need is this: Cold Spring Harbor under Demerec is fairly well known as a laboratory specializing on deficiencies in relation to genetics. Ephrussi's laboratory is fairly well known to be concentrating on transplantation phenomena with respect to genetics...”<sup>447</sup>

The letter therefore directed Haldane to plan research for his group which would contribute to solving an overall problem. The group would therefore specialise in one area and work as a collaborative unit. Since the funding would be made in Haldane's name, he would be expected to manage the programme. The structure that the RF encouraged was therefore hierarchical. The research problems it encouraged recipients to tackle were long-term problems. These were likely to be those with wider applicability, as previously discussed. What Tisdale's letter did not do, however, was direct Haldane towards investigating any particular problem. The whole of academic genetics was within the RF's funding programme, so it had no need to direct Haldane towards certain types of work.

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<sup>446</sup> Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL.

<sup>447</sup> Tisdale to Haldane, December 13, 1937, b26, Haldane papers, UCL.

Tisdale's letter also explained the process for gaining long-term support from the Foundation. This included revealing the support other bodies were prepared to offer, working out the number of personnel required and calculating the total funding required for the programme. This enabled the Foundation to calculate how much money it needed to provide for the programme to be implemented.<sup>448</sup> It allowed the Foundation to assess the value they would get from their investment. It also enabled the RF to judge whether another funding body was likely to take responsibility for funding the project once it was established.

Haldane replied to Tisdale that the group's main area of interest was population genetics, but he also wanted to research developmental genetics and physiological genetics.<sup>449</sup> Still not having received quite the information he wanted, Tisdale sent Haldane a *proforma* based on information contained in Haldane's past letters, with spaces where he required more information.<sup>450</sup> The *proforma* divided the research Haldane had indicated he wanted to conduct into four areas: population studies, developmental genetics, bio-chemical genetics and human genetics. These were further sub-divided. Population studies by organism and human genetics by problem, such as mutation rates. Tisdale indicated that developmental and bio-chemical genetics should also be sub-divided in some manner. This letter further directed Haldane towards a programme of research. By only using information Haldane had previously provided, Tisdale was again careful not to suggest what the content of the programme should be, only what form it should take. At the end of January 1938, Tisdale received the desired scheme.<sup>451</sup>

The relationship between Haldane and Tisdale as shown through this exchange is one of mutual dependence. Both Tisdale and Haldane had the same objective; for the RF to fund Haldane; and both were vital to its realisation. Tisdale was needed to present Haldane's claim for funding to the Foundation. He knew what sort of information it required to take the request seriously. Haldane's continued input was important to make Tisdale's presentation credible. Tisdale wrote to Haldane:

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<sup>448</sup> Tisdale to Haldane, December 13, 1937, b26, Haldane papers, UCL.

<sup>449</sup> Haldane to Tisdale, 18 December 1937, b26, Haldane papers, UCL.

<sup>450</sup> Tisdale to Haldane, December 21, 1937, b26, Haldane papers, UCL.

<sup>451</sup> Haldane to Tisdale, 27 January 1938, f579, b45, s401D, RG1.1, RFA.

“Before I get to the top in the presentation of such recommendation as may be made for assistance to you, I will need to have some tabulations which can be far more effectively presented over your signature than they can over mine.”<sup>452</sup>

In Chapter One (section 1.5) I discussed the idea, current in the secondary literature, that the RF tried to direct the work and organisation of scientists. This section shows that the Foundation did not push a particular area of work onto the scientists they supported. However, it encouraged them to plan long-term work. This favoured research problems with wide applicability. The appearance that the Foundation encouraged ‘American’ work was possibly due to its reliance on American scientists’ opinions of whether non-American scientists were worthy of support. Haldane’s credentials were verified by the American geneticists, T.H. Morgan and C.C. Little.

Haldane’s case shows that since academic genetics conformed to the experimental biology programme, the Foundation was more concerned with academic geneticists’ credentials and stability than the particulars of their research. The Foundation’s officers were more concerned that Haldane had a programme of research than what it was.

The Foundation failed to change their method of funding Haldane from short-term to long-term at this time. In 1938 Haldane contemplated moving to Cambridge when Punnett retired from the Chair of Genetics, if offered the job. Thus, despite gaining his own Chair and Department, Haldane’s position at UCL was still not stable.<sup>453</sup> The Foundation therefore made him a two-year grant in 1938 at the same rate as before.<sup>454</sup>

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<sup>452</sup> Tisdale to Haldane, December 13, 1937, b26, Haldane papers, UCL.

<sup>453</sup> Tisdale’s diary, February 5, 1938, f579, b45, s401D, RG1.1, RFA.

<sup>454</sup> Grant-in-Aid 38035, f578, b45, s401D, RG1.1, RFA.

### 3.2.2.5 A Contractual Agreement

The negotiations I have so far discussed were mainly between Haldane, Watson and the RF. In this section I demonstrate that the funding agreement was actually between the RF and UCL.

In September 1939 Haldane wrote to Weaver asking if it was acceptable for him to administer the NS grant if the research moved site due to the war, as he would have more contact with his researchers than the College would.<sup>455</sup> Both Miller and Weaver replied that this should be acceptable.<sup>456</sup> Haldane replied that the College had refused to give him the money and asked for advice.<sup>457</sup> Weaver replied:

“Our grants are always made to the institutions themselves, although specified for the work of certain individuals; and the administration of such grants must, of necessity, rest with the institution.”<sup>458</sup>

The relationship that existed between Haldane and the RF was therefore a complex one. Weaver’s letter shows that the funding contract was between the RF and UCL, not the RF and Haldane. The Foundation gave UCL money on the condition they supported Haldane to do specific work agreed by Haldane and the Foundation in advance. This form of contract made the university take responsibility for the scientist and their research. This was important for avoiding the kind of dependency issues that arose in Haldane’s case.<sup>459</sup> It was also important for ensuring the research’s long-term survival. The Foundation ideally wanted another body to take full responsibility for the work in future, so it could continue while the RF supported new innovations elsewhere.

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<sup>455</sup> Haldane to Weaver, 22 September 1939, f579, b45, s401D, RG1.1, RFA.

<sup>456</sup> Miller to Haldane, September 30, 1939, f579, b45, s401D, RG1.1, RFA. Weaver to Haldane, October 20, 1939, f579, b45, s401D, RG1.1, RFA.

<sup>457</sup> Haldane to Tisdale, 7 October 1939, f579, b45, s401D, RG1.1, RFA.

<sup>458</sup> Weaver to Haldane, November 3, 1939, f579, b45, s401D, RG1.1, RFA.

<sup>459</sup> The dependency that occurred was of Haldane’s researchers, who the College did not officially employ, rather than Haldane himself, whose employment was guaranteed by the College. The RF normally avoided any form of dependency by requiring matching funds to be provided.

The RF's desire to innovate can be seen in Haldane's case. The Foundation was prepared to support him on a short-term basis until his future at UCL was assured. This support assured the future of academic genetics activities in Britain. The Foundation had no interest in supporting his every-day work, however, and so it would not continue short-term grants once his future at UCL was assured. However, it was interested in supporting his development of an academic genetics programme in Britain. The Foundation therefore saw itself as supporting and innovating change, rather than supporting the everyday work of science.

#### **3.2.2.6 The Rockefeller and the DoZ/B in Conclusion**

In section 3.2.2 I show that the RF was interested in supporting innovative academic research programmes. The RF judged Haldane to be one of the best bets for creating such a programme in Britain. This was because he was highly thought of by eminent academic geneticists in America and because he was one of only a few geneticists working in a location that allowed academic genetics activities.

The Foundation wanted to support research with wide applicability, as this was most likely to reveal something significant about the vital processes. It considered that such research required a group of researchers to work as a collaborative unit over a long-period to gain useful results. The RF therefore expected to receive a research programme that reflected this before it would offer long-term aid. This is clearly seen through Tisdale's negotiation of a programme with Haldane in 1937/1938.

The RF would not support a programme it thought was likely to be abandoned. To provide long-term aid the RF therefore required assurances of the main recipient's stability. The Foundation's frustration in providing Haldane with long-term support was due to it not receiving such assurances. The way the RF supported Haldane also encouraged stability. By giving the grant to UCL the RF tried to encourage the university to take responsibility for Haldane. This helped to ensure that his work had a long-term future that did not necessarily involve the



Foundation. This allowed the RF to continually support innovation and to avoid issues of dependency, which did not help it to maintain a benign appearance. Such issues arose in Haldane's case because the RF providing him with short-term funding without its normal condition of matching funds.

The RF was only prepared to offer short-term aid where the research was likely to develop into a long-term programme of academic genetics. The Foundation believed Haldane's research could develop this way. It therefore funded him annually between 1935 and 1938 to keep the possibility alive but refused to provide short-term funding after he gained a stable position.

While the Foundation wanted to support long-term academic research, it was not concerned what specific academic problem was tackled. Tisdale therefore did not direct the specific content of Haldane's research plan.

The effect of the Rockefeller on Haldane's group was firstly to enable its continued existence. During the 1930s the British academic system was not organised in such a way that it could support a group of geneticists. No other academic location had so many geneticists working at it. The DoZ/B could only support so many because of the RF's aid. This made the group dependent upon the RF. The prospect of long-term NS funding also led Haldane to plan his group's work. Though he never received long-term funding, Haldane's group began to specialise in population genetics at the same time he planned a programme of research for the RF.

### **3.2.3 The RF and the IAG**

This section shows that the qualities the RF looked for at the DoZ/B, namely academic genetics activity, high quality geneticists, stability, university involvement, value for money and the presence of a research programme, were also major factors in determining the funding the RF provided at the IAG. The situation at the IAG was far more complicated than at the DoZ/B, however, due to the influence of another funding body, the ARC, which had different concerns.

### 3.2.3.1 A Cool Relationship

The relationship between Crew and the Rockefeller philanthropies was far more developed at the start of the 1930s than that between Haldane and the philanthropies. The incorporation of the IAG<sup>460</sup> into Edinburgh University had been funded by the IEB. However, the RF provided no support for genetics at the IAG during the 1930s until 1937. In this section I demonstrate that this was because the Foundation was not interested in supporting changes in the Institute's administration or sub-standard research. The RF also made it clear that it was not prepared to fund breeding genetics activities. Though the RF did not fund the IAG in the first seven years of the 1930s, its officers continued to visit the IAG and keep themselves informed of its activities. I argue that this was because the IAG was one of the few British locations where academic genetics activities occurred.

In October 1930 Crew wrote to the RF about the possibility of obtaining funding to equip the IAG's farm and to support veterinary physiology and animal husbandry sections at the Institute.<sup>461</sup> In June 1931 the RF officer, L.W. Jones, visited the IAG regarding the proposal. Jones's impression during the visit was that Crew wanted RF funding to make the Institute free-standing so it was no longer subject to university and governmental control.<sup>462</sup> The issue of the Institute's administration had come into question when the IEB funded the Institute's incorporation into the university. Crew seems to have thought that the incorporation would remove the power of the Joint Committee to direct the IAG. However, he wrote to the IEB:

"It seems quite definite that so long as the income of this department is derived from Governmental sources, there must be a committee with power to direct and control."<sup>463</sup>

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<sup>460</sup> Then the Animal Breeding Research Department.

<sup>461</sup> "I.M." to Jones, May 1, 1931, f44, b4, s405D, RG1.1, RFA.

<sup>462</sup> Jones's diary, June 3, 1931, RG 12.1, RFA.

<sup>463</sup> Crew to Mann, 25 May 1926, f570, b40, s2, IEBA.

Though the Board preferred the Institute to be under university administration, it had a policy of not interfering with internal politics.<sup>464</sup> In section 3.2.2.5 I showed that the RF also had this policy. This was probably sufficient reason for the RF to decline Crew's request. Moreover, Jones had the impression that the IAG functioned well under the current administration.<sup>465</sup>

In September 1931 Jones wrote to Crew that any official request for aid would be declined. The reason he gave was that since the re-organisation of the Rockefeller philanthropies work in the field of agricultural science, including animal breeding, had been drastically reduced. The proposals Crew had discussed in his recent letters were therefore outside the Foundation's funding programme.<sup>466</sup> The letter shows that by 1931 the RF was not interested in supporting breeding genetics activities. It also demonstrates that the Foundation distinguished between breeding and academic genetics activities.

The RF declined the IAG's next request for aid because the research was deemed sub-standard. In 1932 the ARC inspected the IAG and withdrew support for Alan Greenwood's work. Greenwood had been a Rockefeller Fellow in 1931, which suggests that the RF valued both his work and him as a geneticist. Crew turned to the Foundation again for aid<sup>467</sup> and once more the Foundation declined his request.<sup>468</sup> The RF took the opinions of the scientists who had reported on the Institute in 1932 very seriously. If the ARC thought Greenwood's research was not worth backing, the Foundation's officers would have had a difficult time persuading the Trustees that it was worthy of support. The case shows parallels to the RF's consideration of Joseph Needham's and C.H. Waddington's funding proposal for an Institute of Mathematico-Physico-Chemical Morphology during the 1930s. Pnina Abir-Am has shown that the Foundation was keen to support the type of research Needham and Waddington proposed. They did not receive Foundation funding however due to a number of high-profile scientists telling the

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<sup>464</sup> Rose to Mann, June 2, 1926, f570, b40, s2, IEBA.

<sup>465</sup> Jones's diary, June 3, 1931, RG 12.1, RFA.

<sup>466</sup> Jones to Crew, September 4, 1931, f44, b4, s405D, RG1.1, RFA.

<sup>467</sup> Miller's diary, November 17, 1932, RG 12.1, RFA.

<sup>468</sup> Miller's diary, April 28, 1933, RG 12.1, RFA.

RF that Needham and Waddington were not worth supporting.<sup>469</sup> Greenwood's case, like that of Needham and Waddington, and that of Haldane, confirms the Foundation's desire to support excellent scientists and its dependence on those it already deemed excellent to determine who such people were.

Though the RF did not fund Greenwood, one of the Foundation's officers, H.M. Miller, visited Crew again and expressed his regret the RF could not help. Miller met many of the Institute's staff on his visit.<sup>470</sup> Thus, while the Foundation was not keen to help, it wanted to remain on friendly terms. Furthermore, it valued Crew's opinions. When Crew gave Jones an unfavourable opinion of the mycologist, Malcolm Wilson, in June 1931, Jones decided not to visit or fund Wilson.<sup>471</sup> Crew, like Haldane, therefore formed part of the RF's intelligence network, which kept them informed about who was researching what and who was worth supporting.

Though the Foundation refused Crew's first two requests during the 1930s, it was not opposed to funding the Institute *per se*. This is shown by its attempts to remain informed as to the Institute's research. Its continued interest in the Institute was probably because academic genetics research was conducted there. In 1934 the Foundation asked two of its visiting professors to report on the research occurring at the IAG. As well as reporting that a mixture of academic and breeding genetics research was occurring, both reported they were not impressed with the quality of the work. Their views supported those the Foundation already held.<sup>472</sup> The RF's failure to support the IAG at this time was therefore mainly due to its concern regarding the quality of the research.

The Foundation's officers continued to visit Crew, however, and ask for his opinion on the work of various people.<sup>473</sup> On one such visit Crew enquired about

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<sup>469</sup> Abir-Am, 1982. Abir-Am, 1988.

<sup>470</sup> Miller's diary, April 28, 1933, RG 12.1, RFA.

<sup>471</sup> Jones's diary, June 3, 1931, RG 12.1, RFA.

<sup>472</sup> Tisdale to Weaver, September 24, 1934, f44, b4, s405D, RG1.1, RFA. For the opinion of visiting professor, Tage Kemp, see Kemp to Tisdale, August 10, 1934, f44, b4, s405D, RG1.1, RFA.

<sup>473</sup> Weaver's diary, May 11, 1935, RG 12.1, RFA. Miller's diary, December 6 and 7, 1935, RG 12.1, RFA.

the possibility of a fellowship at Caltech for one of his *Drosophila* workers. Miller judged the woman, Rowena Lamy, to have an unsuitable personality for Caltech and to be too old to benefit much from the experience.<sup>474</sup> This demonstrates that fellowships were intended to train people at the start of their careers. This was a form of long-term investment for the RF.

### 3.2.3.2 Redeveloping a Funding Relationship

In 1937 the RF began funding genetics research at the Institute again. In this section I study the first two grants it awarded the Institute. I show that both were for academic genetics research and both were awarded to researchers who were highly esteemed. The Foundation therefore funded genetics at a breeding location when it found academic research and high quality researchers to support. The RF's concern with stability and another funding body taking over support at a latter date is also shown from the negotiations that occurred over H.J. Muller's grant.

In 1937 one of the IAG's researchers, P.C. Koller, applied for a Rockefeller Fellowship.<sup>475</sup> Miller visited the Institute in April 1937 to meet him. Miller concluded that Koller would probably benefit greatly from the experience and that it would also probably benefit the Institute generally.<sup>476</sup> In October 1937 Koller left for Caltech.<sup>477</sup>

Koller was one of the more academic researchers in the Department, researching how the X and Y chromosomes pair in meiosis so as to maintain their heterogeneity. His work is described in more detail in Chapter Five (especially section 5.4.3). The Foundation therefore agreed to support the training of a respected academic geneticist in the Institute partly because it would benefit the Institute. In which way is not stated; however, since the RF were concerned about the quality of the IAG's research and Koller would be trained by top

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<sup>474</sup> Miller's diary, December 6 and 7, 1935, RG 12.1, RFA.

<sup>475</sup> Koller to Darlington, 9 April 1937, folder J126, box c.110, Darlington papers.

<sup>476</sup> Miller's diary, April 13, 1937, RG 12.1, RFA.

<sup>477</sup> Fellowship 37079, Natural Sciences Fellowship Recorder Cards, RFA.

American academic geneticists, it seems reasonable to assume he was expected to introduce higher standards to the academic genetics group on his return.

In November 1937 the work of the Institute became more focused on academic activities as the highly esteemed cytogeneticist, H.J. Muller, began work there.<sup>478</sup> The Institute did not have sufficient means to keep Muller. All they could offer were working facilities, free bed and board and whatever small income the Macaulay shares were producing.<sup>479</sup> In autumn 1937 Muller and Julian Huxley, who had encouraged Muller to come to Britain,<sup>480</sup> visited the RF about funding Muller's employment at Edinburgh.<sup>481</sup> Crew did not approach the Foundation for aid until February 1938.<sup>482</sup> This may be because, given the past history, Crew thought the Foundation unlikely to help. However, before going to America, Koller thought that Crew did not particularly want Muller there.<sup>483</sup>

The Foundation had two options for funding Muller's employment. It could award him a grant-in-aid, such as those awarded to Haldane. However, it was only prepared to offer these where the award-holder had a permanent position. The Rockefeller official, F.B. Hanson, made it clear to Muller that because he did not have a permanent position any request for *long-term* aid would be declined.<sup>484</sup> Hanson wrote to Tisdale that short-term aid could be considered on its merits if Muller applied for it.<sup>485</sup> The RF could alternatively treat Muller as a refugee. The Trustees had restricted such aid to fixed-period grants where a

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<sup>478</sup> Muller was offered a post at the JI in June 1937. He accepted it on the condition that he was given £100-200 more salary. The Trustees turned him down. (Miller's diary, June 28 - July 1, 1937, RG 12.1, RFA). This left Muller with few options for working in Britain. Punnett was still in the Chair at Cambridge and not welcoming of other geneticists. Haldane was attempting to keep his department going on the limited budget that the Weldon Fund provided. This left Edinburgh as the only major genetics location open to Muller.

<sup>479</sup> Crew to The Secretary of the RF, 17 February 1938, f44, b4, s405D, RG1.1, RFA. For a discussion of the Macaulay shares see section 3.3.2.1.

<sup>480</sup> Huxley to Darlington, 3 November 1936, folder J.107, box c.109, Darlington papers.

<sup>481</sup> Muller to Hanson, February 11, 1938, f44, b4, s405D, RG1.1, RFA.

<sup>482</sup> Crew to The Secretary of the RF, 17 February 1938, f44, b4, s405D, RG1.1, RFA.

<sup>483</sup> Koller to Darlington, 11 April 1937, folder J.126, box c.110, Darlington papers. Crew wrote to Tisdale however: "This particular matter possesses such great importance to me at least, that naturally I was inclined to be very pessimistic, half expecting that my request would be promptly turned down." (Crew to Tisdale, 6 April 1938, f44, b4, s405D, RG1.1, RFA). This was at the time when Crew was trying to obtain funds for Muller, however, and so perhaps his views had changed with time.

<sup>484</sup> Hanson to Muller, February 28, 1938, f44, b4, s405D, RG1.1, RFA.

<sup>485</sup> Hanson to Tisdale, 1 March 1938, f44, b4, s405D, RG1.1, RFA.

permanent position was guaranteed at its termination. Muller did not have such an assurance. Tisdale therefore arranged to see Crew to discuss the situation further.<sup>486</sup>

Having received assurances from Muller that he wanted to stay at Edinburgh, Tisdale met the Principal of the university, the Chairman of the Animal Breeding Committee, the Secretary of the university and Crew. Tisdale told them that the Rockefeller would only fund Muller's employment if he was offered a permanent position, if the university paid something towards Muller's salary from the beginning and if it agreed to assume total responsibility for the salary within a short period. These conditions were designed to ensure the grant paid for Muller's transfer to a permanent position at Edinburgh and that the university was fully committed to this plan from the start.

At the meeting it was agreed that both Tisdale and the Principal of Edinburgh University, Sir Thomas Holland, would work towards an agreement whereby the University Court would offer Muller a position he would accept and the RF would provide £1200 towards his salary. The amount would be £500 in the first year, reducing by one hundred pounds a year to £300 in the third and last year.<sup>487</sup>

In May 1938 the Secretary of Edinburgh University confirmed that the university was prepared to offer Muller a lectureship and take responsibility for paying him £700p.a. if the Rockefeller provided £1200 as previously discussed. Muller had also indicated he would take the job.<sup>488</sup> At the end of June the RF approved the grant.<sup>489</sup>

### 3.2.3.3 Muller and the Rockefeller

While Koller was on his RF fellowship, he and Muller began planning the expansion of the Institute's *Drosophila* research.<sup>490</sup> The RF refused to fund this

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<sup>486</sup> Crew to Tisdale, 6 April 1938, f44, b4, s405D, RG1.1, RFA.

<sup>487</sup> Tisdale's diary, April 30, 1938, f44, b4, s405D, RG1.1, RFA.

<sup>488</sup> Fleming to The Secretary of the RF, 20 May 1938, f44, b4, s405D, RG1.1, RFA.

<sup>489</sup> Grant-in-Aid 38068, f44, b4, s405D, RG1.1, RFA.

<sup>490</sup> Miller's diary, September 21, 1938, RG 12.1, RFA.

expansion. In this section I show that this was because it would have had to let Edinburgh break one of the clauses in a previous contract, which would have set a poor precedent, and because it was concerned with the stability of Muller's position.

In October 1938 Koller returned from his Fellowship.<sup>491</sup> At the end of October the pair visited the Rockefeller's Paris office to discuss a grant for equipment and assistants for the expansion.<sup>492</sup> The officer they saw, H.M. Miller, told them that Tisdale, the officer responsible for such requests, would visit Edinburgh shortly but it would probably be easier for the Foundation to provide funding for equipment than for assistants.<sup>493</sup> This was presumably because the equipment was a long-term investment and because the Foundation took responsibility for those it supported, as discussed below. The Trustees would have been reluctant to support assistants whose future was not assured.

In November Miller visited the Institute. He told Crew he could not comment on the likelihood of Muller and Koller's request being accepted. However, Miller reminded Crew that he had assured the Foundation he could meet Muller's research needs when it agreed to help with Muller's salary.<sup>494</sup> Nevertheless, Muller and Koller presented Miller with a proposal for the expansion.<sup>495</sup> The proposal shows that at least one of them, probably Muller, was adept at writing funding proposals. The proposal laid out the lines of work the pair wished to concentrate on, the total cost of it, how much money was available from local sources and how much money the Foundation was being asked to provide.<sup>496</sup> This is all the information Tisdale told Haldane the Foundation would require to consider major support of his work.<sup>497</sup> It was also laid out in a manner similar to the *proforma* Tisdale created for Haldane.<sup>498</sup> Muller therefore knew that the Foundation would want him to present: first, a programme of research, second,

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<sup>491</sup> Fellowship 37079, Natural Sciences Fellowship Recorder Cards, RFA.

<sup>492</sup> Miller's diary, October 28, 1938, RG 12.1, RFA.

<sup>493</sup> Miller's diary, October 28, 1938, RG 12.1, RFA.

<sup>494</sup> Miller's diary, November 21, 1938, RG 12.1, RFA.

<sup>495</sup> Tisdale's diary, November 30, 1938, f44, b4, s405D, RG1.1, RFA.

<sup>496</sup> Memorandum, 12/12/38, f44, b4, s405D, RG1.1, RFA.

<sup>497</sup> Tisdale to Haldane, December 13, 1937, b26, Haldane papers, UCL.

<sup>498</sup> Tisdale to Haldane, December 21, 1937, b26, Haldane papers, UCL.



what commitment was available from other sources and third, how much money the RF would have to provide.

Muller seems to have believed that once his position was assured the Foundation would award him a grant-in-aid. Hence Muller's and Koller's funding proposal. Hanson's letter in February 1938 had implied as much.<sup>499</sup> Koller had also told Crew, and presumably Muller, that when he visited the New York office at the end of his fellowship, they had assured him that such a request would be treated sympathetically.<sup>500</sup> The New York office was possibly unaware of Crew's assurance that he could provide fully for Muller's research needs when the original grant for Muller was negotiated.<sup>501</sup> Given this, Tisdale's rejection of the proposal was fairly inevitable. Awarding a new grant would have implied it was acceptable for the Institute not to meet its obligations to the Foundation. This would have set a poor precedent.

Furthermore, Tisdale was not certain of Muller's future. Providing the Institute with equipment for Muller was only sensible if it was likely he would remain there. Both Muller and Crew tried to assure the Foundation that he would. Muller told Miller that he expected, and wanted, to remain at Edinburgh. Both Muller<sup>502</sup> and Crew also emphasised that the Cambridge Chair was likely to be suppressed when Punnett retired so Muller was unlikely to move to Cambridge.<sup>503</sup> Tisdale, however, wondered whether Crew would be happy accommodating Muller if Muller had most of the money and students. Tisdale also wondered whether Muller would be happy remaining under Crew if he was in charge of most of the students and money. Muller had not stayed at any one institute for very long so far in his career and there was no reason to believe Edinburgh would be any different. Tisdale therefore told Crew that he would prefer to wait for another year to see how Muller settled in before making another grant.<sup>504</sup>

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<sup>499</sup> Hanson to Muller, February 28, 1938, f44, b4, s405D, RG1.1, RFA.

<sup>500</sup> Tisdale's diary, November 30, 1938, f44, b4, s405D, RG1.1, RFA.

<sup>501</sup> Tisdale's diary, November 30, 1938, f44, b4, s405D, RG1.1, RFA.

<sup>502</sup> Miller's diary, November 21, 1938, RG 12.1, RFA.

<sup>503</sup> Tisdale's diary, November 30, 1938, f44, b4, s405D, RG1.1, RFA.

<sup>504</sup> Tisdale's diary, November 30, 1938, f44, b4, s405D, RG1.1, RFA.

In June 1939 Miller visited the Institute again. He discovered that Crew was annoyed with Muller. Muller had recently re-married and was spending much of his time looking after his wife, who had pulmonary tuberculosis. Koller was also being distracted from work by his private life. While Crew thought that Muller's and Koller's work had deteriorated, Muller had his own grievances. The Institute was making PhD positions conditional upon completing the Institute's new BSc program. This meant Muller was unlikely to have many PhD students for a couple of years. Muller argued this increased his and Koller's need for technical assistants.<sup>505</sup> However, under these uncertain circumstances the RF was not prepared to re-evaluate Muller and Koller's proposal.

#### 3.2.3.4 Emergency Aid

On 3 September 1939 Britain declared war on Germany. At the time the Seventh International Congress of Genetics, which was held at the Institute, had just ended.<sup>506</sup> Two of the Polish Congress attendees, Mr and Mrs Slizynski, became trapped in Britain. Koller advised them to return to Edinburgh.<sup>507</sup> Crew approached many bodies to gain support for the Slizynskis. One was the RF, who had previously awarded Mr. B.M. Slizynski a fellowship and so had previously indicated its interest in his research.<sup>508</sup> My discussion of the RF's funding of the Slizynskis in this section shows that the RF was still concerned with stability and long-term research during the Second World War, but that it had to redefine its understanding of these concepts.

At the end of September 1939 Miller told Crew there was no mechanism for the RF to help refugees such as the Slizynskis. Fellowships required the assurance of a permanent job to return to. This was clearly not the case for the Slizynskis. The RF's concern with stability therefore initially prevented RF aid in this case. However, Miller promised to forward the request to the head office in New York.<sup>509</sup> On receiving it, Weaver pushed the trustees for a general policy that

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<sup>505</sup> Miller's diary, June 6, 1939, RG 12.1, RFA.

<sup>506</sup> Punnett, 1941, 1.

<sup>507</sup> Koller to Demerec, 20 September 1939, folder Koller, Peo C#1, Demerec papers.

<sup>508</sup> Crew to The Secretary of the RF, 18 September 1939, f44, b4, s405D, RG1.1, RFA.

<sup>509</sup> Miller to Crew, September 28, 1939, f45, b4, s405D, RG1.1, RFA.

under the current circumstances the Foundation could award emergency aid without assuming responsibility for the recipients' future.<sup>510</sup> Weaver was thus pushing for funding to be awarded for research without the normal goal of training a geneticist for the future.

Two days later Miller enquired whether the Slizynskis had obtained funding elsewhere.<sup>511</sup> Muller replied that they were still at Edinburgh without funds. Muller also encouraged the Slizynskis to write to Miller.<sup>512</sup> In their letter the Slizynskis wrote that Mr Slizynski was likely to be mobilised for war at the start of December but that Mrs Slizynski, who was also a scientist, was likely to remain.<sup>513</sup>

At the same time the Slizynskis wrote to Miller, the New York office authorised Miller to award them \$1000.<sup>514</sup> On receiving authorisation in November 1939 Miller telephoned Crew to inform him that a grant for the Slizynskis was likely.<sup>515</sup> However, on receiving the Slizynskis' letter and discovering Mr Slizynski would probably be called up at the start of December, Miller wrote to Crew informing him that it was not possible to help the Slizynskis for so short a period of time.<sup>516</sup> Though the RF was, on this occasion, prepared to help in an uncertain situation, it was not prepared to help for a period of time it considered too short to gain useful scientific results.

On receiving Miller's letter, Crew advised Mr Slizynski to see the Polish Consulate to find out when he would be called up. Slizynski received a certificate from the Consulate stating he would not be called for war work until December 1940.<sup>517</sup> Crew then suggested that Koller and Muller wrote to Miller providing details of the work the Slizynskis were doing.<sup>518</sup> However, Muller's and Koller's letter was unnecessary. The Foundation's concerns were only regarding the time

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<sup>510</sup> Weaver to "TBA, FBH, WW, JWG, WCH", October 19, 1939, f45, b4, s405D, RG1.1, RFA.

<sup>511</sup> Miller to Muller, October 21, 1939, f45, b4, s405D, RG1.1, RFA.

<sup>512</sup> Muller to Miller, October 27-28, 1939, f45, b4, s405D, RG1.1, RFA.

<sup>513</sup> B.M. Slizynski and Helen Slizynski to Miller, October 27, 1939, f45, b4, s405D, RG1.1, RFA.

<sup>514</sup> Weaver to Miller, 27 October 1939, f45, b4, s405D, RG1.1, RFA.

<sup>515</sup> Miller's diary, November 10, 1939, RG12.1, RFA.

<sup>516</sup> Miller to Crew, 18 November 1939, f45, b4, s405D, RG1.1, RFA.

<sup>517</sup> Crew to Miller, 7 December 1939, f45, b4, s405D, RG1.1, RFA.

<sup>518</sup> Muller and Koller to Miller, 9 December 1939, f45, b4, s405D, RG1.1, RFA.

period of the grant. On receiving Crew's letter stating that Mr. Slizynski would remain at Edinburgh for at least another year, Miller confirmed that the Foundation would provide \$1000 to support the Slizynskis for the year beginning 1 December 1939.<sup>519</sup>

### 3.2.3.5 Trying to move: the case of H. J. Muller

At the end of 1939 the Foundation was also faced with Muller's attempts to move to America. In this section I show that the RF's grants were designed to make it difficult for the scientists it supported to move. This encouraged them to finish the programmes of research the RF supported.

At the start of the Second World War, the future of the IAG became very uncertain. Crew was on the active list,<sup>520</sup> and the Institute's buildings seemed likely to be taken over for bacteriological research.<sup>521</sup> The Institute was fighting for its survival. It attempted to do so by concentrating on teaching rather than research. In September 1939 Koller wrote:

"Under the present circumstances, we will be unable to carry on research on large scale, our job is to keep genetics alive in our University. Director is on the active list and he will leave us very soon, probably will go abroad – the teaching of genetics left to me and Donald. This, two of us can do and Muller would waste only his time by staying behind – and he is not keen to stay. His wife is his only concern now on."<sup>522</sup>

Although Muller's wife was declared a friendly alien,<sup>523</sup> at the start of the war Muller seems to have worried that she would be interned since she was German.<sup>524</sup>

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<sup>519</sup> Miller to Crew, December 12, 1939, f45, b4, s405D, RG1.1, RFA. For details of the grant see Grant-in-Aid 39169, f44, b4, s405D, RG1.1, RFA.

<sup>520</sup> Koller to Darlington, 14 September 1939, folder J.131, box c.110, Darlington papers.

<sup>521</sup> Koller to Demerec, 20 September 1939, folder Koller, Peo C#1, Demerec papers.

<sup>522</sup> Koller to Darlington, 14 September 1939, folder J.131, box c.110, Darlington papers.

<sup>523</sup> Carlson, 1981, 269.

<sup>524</sup> Carlson, 1981, 258.

In September 1939 Muller tried to find a new position in the United States, which was not then at war. The Harvard geneticist, M. Demerec, told the New York Rockefeller official, F.B. Hanson, he would employ Muller if the Foundation covered his salary and research expenses. Hanson replied that contrary to Demerec's perception it was not possible to transfer Muller's current grant to another institution and that it did not cover all of Muller's salary or any of his expenses in any case.<sup>525</sup> RF grants, as seen in Haldane's case, were made to the university not the individual, which made them non-transferable. This encouraged the university to take responsibility for the individual and made it less likely the scientist would move location as they could not transfer their grant. This helped create stability, which the RF considered important for conducting long-term research. It also meant the RF only paid for scientists to work in known conditions. The RF would not end up paying for a scientist to conduct work in unsuitable conditions because the scientist changed location half-way through a long-term grant.

#### **3.2.3.6 The Rockefeller and the IAG in Conclusion**

The relationship between the Rockefeller and the IAG was an uneasy one during the 1930s. The Foundation was interested in the location because it conducted some academic genetics activities. However, it was unwilling to fund its conversion to a fully academic location. This would have involved it taking over responsibility for the entire Institute from the ARC, as Crew proposed in 1930. Doing so would have made the Foundation look less than benign, as it would have poached a functioning institute from another funding body's control. Without taking over responsibility for the funding from the ARC, the Institute had to be administered by the Animal Breeding Committee, as Crew made clear in 1926. The Committee ensured that the location, set up as part of the DC's programme for agricultural research, retained its animal breeding research function.

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<sup>525</sup> Hanson's diary, September 25, 1939, f45, b4, s405D, RG1.1, RFA.

Though the Foundation was interested in the academic research occurring at the IAG it funded little work there during the 1930s, with all of its grants clustered towards the end of the decade. There were several reasons for this. Firstly the Foundation was uninterested in supporting breeding genetics activities. The initial proposals Crew put to the RF were for breeding activities. Secondly, the IAG's work was not considered top-class. The ARC's opinion of the Institute was taken seriously by the RF. Once the Council withdrew its support from Greenwood the RF would not support him either. The 1934 reports of the Foundation's travelling professors confirmed the RF's view that the quality of the Institute's work was not excellent.

In contrast to this, the projects the RF supported at the end of the decade were academic genetics activities conducted by highly esteemed geneticists. Miller wrote of Koller, "K.[oller] is unquestionably outstanding in research..." Mr. Slizynski had previously received a Rockefeller Fellowship, while H.J. Muller was considered one of the best geneticists in the world. The quality of the researcher was important in assuring the Trustees that they were getting value for money. It was for the purposes of being able to judge the quality of different researchers that the Foundation maintained an intelligence network, of which both Crew and Haldane were part.

The funding proposal Koller and Muller put forward in 1938 was not, however, rejected because it was for breeding research or because of their reputations. It was rejected, firstly, because funding Muller's research would have let Edinburgh break one a condition of a previous Foundation grant. This would have set a poor precedent. Secondly, the Foundation was not convinced Muller's position at Edinburgh was stable. The importance of stability to the Foundation was seen in Haldane's case. It also influenced the conditions of the grant for employing Muller, such as the guarantee of a permanent position after three years. The RF encouraged stability by making the grants to universities. Thus, Muller's grant could not be transferred to another university when he tried to move at the end of 1939. Finally, the RFs concern with stability meant that it had no mechanism to help the Slizynskis at the start of the Second World War, since they had no guarantee of a permanent position.

The RF desired stability for two reasons. Firstly, it took responsibility for the people it supported, as this helped the RF maintain its benign image. The Foundation could not guarantee the future of the assistants Koller and Muller wanted to employ and so Miller thought it more likely the RF would pay for equipment. The other reason for the RFs desire for stability was that it wanted to make long-term investments. The Foundation was therefore not willing to support Muller for three years unless the university agreed to employ him thereafter. The uncertainty brought by the Second World War caused the RF to redefine their concepts of long-term work and stability. While the RF would not support the Slizynskis for a month, it would support them for a year. The funding was provided so they could conduct scientific work, but since they had no guaranteed future position, it did not have the RF's usual goal of training geneticists for the future.

Though the RF did not fund the IAGs separation from the university and ARC funding, its effect was to reinforce the message Crew had taken from the ARC in the early to mid 1930s. This message was that the future of the Institute was not in breeding genetics activities.

### **3.2.4 The Rockefeller in Conclusion**

In section 3.2 I have shown that in considering funding proposals the RF had six main interests: the content of the work to be conducted, the quality of the main recipient, the stability of the main recipient, the presence of a programme of research, the value they would get for their money and the likelihood that another Funding Body would take over responsibility for funding the research.

In terms of the content, the Foundation was interested in funding academic genetics activities and not breeding genetics activities. This was because only the former was of relevance to the NS's funding programme for research into vital processes. The Medical Science Division funded research into applying genetics to medicine, but there was no division that supported its application to breeding.

Within academic genetics, however, the Foundation had little interest in the content of the work.

The Foundation was interested in the quality of the researchers it funded. Haldane received many commendations, while Crew and the IAG were not as highly thought of. This explains in part the difference in Rockefeller funding of the two departments.<sup>526</sup>

The type of research the Foundation wanted to support provided results with broad implications about vital processes. They deemed these to come from long-term work. The Foundation was therefore concerned with the stability of a researcher's position. This prevented the RF from providing Haldane with long-term support throughout the 1930s. The way that the Foundation gave grants encouraged stability for the researchers it aided. The grants were given to the university for a researcher not to the researcher themselves. This made Muller's move much more difficult in 1939, as it was intended to.

The RF would only provide long-term support if a research programme had been formed. The kind of research programme it had in mind was one where a group of researchers collaborated to tackle a coherent, broad, problem. The named funding recipient took responsibility for the overall programme of research, with others taking responsibility for projects conducted within the programme. Though the RF did not succeed in establishing programmes at either the DoZ/B or the IAG, they extracted research programmes from both Haldane and Muller.

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<sup>526</sup> Between 1935 and 1939 inclusive, the IAG received approximately £720 in comparison to the £2650 the DoZ/B received. (The IAG was awarded £1200 over a three year period on June 30, 1938 to subsidise H.J. Muller's wages by £500 in the first year, £400 in the second year and £300 in the third. (Grant-in-Aid 38068, f44, b4, s405D, RG1.1, RFA.) For the period up to the end of 1939 the Institute would therefore have received £500 in the first year and half of the second year's grant of £400, which totals £700. The Institute was also awarded \$1000 from 1 December 1939 for B.M. Slizynski. (Grant-in-Aid 39169, f44, b4, s405D, RG1.1, RFA.) At a conversion of \$4 to £1, which was roughly the rate in 1939, this works out as £250, one month's worth is £20.83. Thus the IAG received approximately £720 from the Foundation for the period 1935-1940. Haldane's section in the DoZ/B was awarded £550 for one year from 15 February 1935 (Grant-in-Aid Paris R.A. Action No. 4, f578, b45, s401D, RG1.1, RFA); £600 for one year from 15 February 1936 (Grant-in-Aid 35254, f578, b45, s401D, RG1.1, RFA); £600 for one year from 15 February 1937 (Grant-in-Aid 37029, f578, b45, s401D, RG1.1, RFA); and £1200 for a two year period beginning July 1, 1938 (Grant-in-Aid 38035, f578, b45, s401D, RG1.1, RFA). Eighteen month's worth of this latter grant is £900 and thus the total amount the DoZ/B received for genetics work between 1935 and 1940 was £2650.)



At this time, the DoZ/B began to specialise in population genetics and work as a collaborative unit. The RF therefore appears to have affected the organisation of academic genetics at the DoZ/B.

The RF was also concerned with the value it would get for its money. Stability was important to this. The RF was not prepared to invest in equipment that might not be utilised if the researcher moved to another location. The quality of the researcher was also important for ensuring value and was one of the reasons the RF maintained an intelligence network. The network ensured the RF was not just supporting good scientists but the ones most likely to provide significant information about vital processes.

Value for money did not necessarily mean that the RF expected to see immediate returns however. As we have seen the Foundation was interested in long-term results. It was prepared to invest in training excellent scientists, such as Koller, to aid their ability to do top quality research in future. Fellows had to have secure jobs to return to, as this ensured they returned to active research. Thus, Greenwood and Koller received Fellowships at the IAG, but none of the researchers at the DoZ/B received one as they did not have secure positions.

The RF's final interest was in whether other bodies were likely to take over funding the work in the future. The Foundation had no interest in funding every-day scientific work, only innovative research. It therefore ensured that Edinburgh University would take over the every-day support of Muller and it refused to give Haldane any more one-year grants once his position at UCL was assured. This was one reason the RF was interested in which other bodies would support the work. It only wanted to support research that would later be fully supported by a university or another funding body. This left the Foundation free to encourage scientific innovation.

The study of the RF's interaction with these two locations shows that the funding situation in the breeding setting was far more complicated than in the academic setting. In the academic setting, the concerns of all the funders more or less coincided. They all wished to encourage academic research, and as section 3.3.1

shows, none wished to dictate the content of the research programme. The RF and Haldane still had some problems in agreeing funding, however, due to the lack of stability in Haldane's position. Both parties were willing to find common ground, and in 1938 they moved towards long-term funding at the location. In the breeding setting, the RF had a more difficult time as it had to contend with the competing demands of the ARC. The Council funded the maintenance of the location in the breeding setting and the RF was not prepared to alter this situation. The ARC funded the employment of permanent staff to conduct a mixture of academic and breeding genetics activities. There was therefore a small amount of convergence between the RFs funding programme and the work of the IAG. Initially the RF did not fund the IAG during the 1930s because of quality concerns, but the Foundation and Crew were willing partners in negotiating the RF's funding of research in the department. Once the quality concerns were dealt with the Foundation funded academic genetics activities at the IAG.

### **3.3 Funding Bodies**

The RF was only one of several funding bodies to support genetics research at the two locations. In this section I compare the funding bodies that supported the DoZ/B and the IAG. This shows how important different bodies' support was to the two locations and thus how much influence these bodies had. It will also show whether there was a general type of body that funded each location's research or if these varied.

#### **3.3.1 The DoZ/B, UCL**

##### **3.3.1.1 Individual funding I: 1933-1935**

When Haldane joined the DoZ in 1933 there was no provision for genetics other than his own salary and research expenses plus the expenses of students. In 1933/34 a group of geneticists built up around him. As I show in this section, these geneticists either had individual funding from non-applied sources or no funding. This resulted in the group's instability and in it conducting research that

could be done cheaply. The former made it difficult for Haldane to plan the group's research.

In August 1933<sup>527</sup> the geneticists, Hans Grüneberg and Ursula Philip, joined the DoZ. Both were German Jews who, by law, were not allowed to work in a German university.<sup>528</sup> Haldane invited the pair to conduct their research at UCL and obtained funding for them for two years from the Central British Fund for German Jewry.<sup>529</sup> The rate was approximately £180 p.a. for Grüneberg and £120 p.a. for Philip.<sup>530</sup> The purpose of the body was to support German Jewish refugees in Britain. At about the same time, Haldane gained two PhD students: Cecil Gordon and A.L.M. Christie. Gordon had a South African grant which ended in December 1934. Christie was not funded.<sup>531</sup>

By October 1934 four other geneticists were working in the department, all with individual or no funding. M. Lafon, had a Caisse Nationale grant to work with Haldane for a year.<sup>532</sup> A Cambridge undergraduate, F.C. Minns, conducted research in the department unfunded.<sup>533</sup> Peter Gorer, who was medically qualified and interested in integrating genetics and medical research,<sup>534</sup> also worked there supported by his father.<sup>535</sup> The final member of the group was the

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<sup>527</sup> As discussed in Chapter Two (section 2.2.2), Lewis and Hunt, 1984, 229 states that Grüneberg began work in August 1933. Since the funding for Grüneberg and Philip came through at the same time it seems likely that Philip also began work in August. A female German refugee was working at the department in September (Miller's diary, September 26, 1933, RG 12.1, RFA). Philip is recorded as being at the Department of Zoology in December 1933 (Miller's diary, December 13, 1933, RG12.1, RFA).

<sup>528</sup> Deichmann, 1996b, 11.

<sup>529</sup> The Joint Foreign Committee to Grüneberg, 10 August 1933, folder Pm-Q, b13, Grüneberg papers.

<sup>530</sup> These are the figures given in: Haldane to Miller, November 3, 1934, f578, b45, s401D, RG1.1, RFA. Grüneberg received a letter from the fund in 1933 stating that his grant would be £125 p.a. (The Joint Foreign Committee, Woburn House to Grüneberg, 10 August 1933, folder Pm-Q, b13, Grüneberg papers). Grüneberg's grant was raised when the committee discovered he was married. (Interview with Grüneberg, Imperial War Museum Sound Archives, reference 004478/03, reel 1). This suggests that Philip's grant was £125p.a. In the interview Grüneberg states that his salary was raised from £187p.a. to £250p.a. Possibly the grant was raised twice, once to approximately £180 and again to approximately £250p.a. because Grüneberg received a second letter from the fund in 1935 stating that they were extending his grant at a rate of £240 p.a. (Professional Committee for German Jewish Refugees to Grüneberg, 16 July 1935, folder Pm-Q, b13, Grüneberg papers).

<sup>531</sup> Haldane to Miller, November 3, 1934, f578, b45, s401D, RG1.1, RFA.

<sup>532</sup> Miller's diary, October 22, 1934, RG 12.1, RFA.

<sup>533</sup> Haldane to Miller, November 3, 1934, f578, b45, s401D, RG1.1, RFA.

<sup>534</sup> Medawar, 1961, 96-97.

<sup>535</sup> Miller's diary, March 14-15, 1934, RG 12.1, RFA.

cytogeneticist, Pius Koller. Koller had left the IAG due to its lack of finances and taken up Haldane's offer of work space at UCL while he found another job.<sup>536</sup> At the end of 1934 he was supported by Haldane and the cytologist, Cyril Darlington.<sup>537</sup>

Four of the geneticists were therefore unfunded. They were supported by family, in the case of Gorer, or friends, in the case of Koller. The four who were funded all had temporary grants. Two of these, Grüneberg's and Philip's, were to support the relocation of German Jewish refugees and had no relation to the type of research the pair conducted. Gordon and Lafon's grants were to allow them to undertake particular projects for a set period of time at the Department. Though the details of Gordon's grant are unknown, both Gordon's and Lafon's grants supported academic genetic activities.

The lack of funding had two results. Firstly, the constraints upon the geneticists' work arose not from the interests of a funding body but from their ability to conduct certain types of research with little money and the facilities available at the Department. This favoured the use of inexpensive organisms such as *Drosophila* and, to a lesser extent, mice.<sup>538</sup> It favoured breeding work over cytological work, which required more expensive equipment. At the end of 1934 Haldane applied to the Rockefeller for funding to purchase two binocular microscopes and one compound microscope, and to pay for the general expenses of the department, by which he meant mouse cages, bottles, food, and staff travel expenses.<sup>539</sup> Thus, Haldane required additional funding to conduct cytogenetics research and to expand the research of the rest of the group. He told the Rockefeller; "general expenses ... are bound to expand."<sup>540</sup>

Since funding bodies had no say over the content of the work conducted, Haldane had a lot of control over it. The work therefore conformed reasonably

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<sup>536</sup> Koller to Darlington, 14 August 1934, folder J.122, box c.110, Darlington papers.

<sup>537</sup> Haldane to Miller, November 3, 1934, f578, b45, s401D, RG1.1, RFA.

<sup>538</sup> The Rockefeller officer, W.E. Tisdale, commented in his diary, "He [Haldane] has on the staff sufficient personnel to take care of his animals (mice) which are not expensive." (Tisdale's diary, October 21 and 22, 1935, f578, b45, s401D, RG1.1, RFA).

<sup>539</sup> Summary of work in Progress, 3 October 1934, f578, b45, s401D, RG1.1, RFA.

<sup>540</sup> Summary of work in Progress, 3 October 1934, f578, b45, s401D, RG1.1, RFA.

well to Haldane's 1932 research plan as discussed in Chapter Two (section 2.2.2). In 1934 Grüneberg conducted the three point linkage test in mice Haldane had planned, Gorer tested for serological differences between mouse strains, Lafon for physiological differences, Gordon conducted experimental population genetics work with *Drosophila* and Koller compared the chromosomes of different races of *Drosophila*. The work of Philip, Christie and Minns also had some evolutionary significance.

The other result of the group having either temporary or no funding was that the group was unstable. This made it difficult to plan the group's research in a programmatic manner. The geneticists working with him may have found more permanently funded work elsewhere at any time and so Haldane did not know what geneticists and thus what skills and interests would be available within his group in future. He also could not advertise for researchers who specialised in areas he wanted to develop, as he had no funding to offer. He therefore had to choose from those who approached him. Haldane had managed to implement his vision of genetics at the DoZ and gather a group of researchers, but without obtaining further funding the group would have dispersed and the research plan would have been abandoned. In the next section I look at how Haldane tried to prevent this from occurring.

### **3.3.1.2 Recurrent funding**

At the start of the 1930s the only official recurrent funding for genetics research at the location was to employ and support Haldane. Watson also provided Haldane with £200-300 for his group's work from the Department's budget.<sup>541</sup> Due to the growth of his group Haldane tried to find additional recurrent funding to support them. From 1935 the RF provided funding that stabilised Haldane's group. In 1937 the recurrent funding Haldane received increased substantially. As I show in this section, Haldane used this money to further increase his group's stability and to increase its productivity.

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<sup>541</sup> Tisdale's diary, October 21 and 22, 1935, f578, b45, s401D, RG1.1, RFA.

By 1937 Haldane thought of the RF's funding as recurrent. He wrote to the Foundation in November 1937: "I sincerely hope you will be able to keep up your £600."<sup>542</sup> Haldane was not asking the Foundation for money to do particular work but to continue providing the money they had over the last two years to keep genetics research going at the location. The Foundation's officers were far more aware that the funding was not officially recurrent. The Trustees could refuse to make more grants to Haldane and were likely to do so if his research did not become programmatic. The officers therefore wished to make a capital<sup>543</sup> or at least a long-term grant<sup>544</sup> to Haldane to ensure his department could be maintained for a number of years. For this they needed Haldane to form a programme of research. This was absent from the department during the early to mid 1930s because of the group's instability, as discussed in section 3.3.1.1 above.

When Haldane became Weldon Professor the value of his group's recurrent funding increased, but not by much. The Weldon endowment brought in approximately £200 p.a. to maintain the Department.<sup>545</sup> Haldane also received £100 more from Watson for the group than before.<sup>546</sup> The DoZ could offer the group extra money as the cost of Haldane's salary was transferred to the Weldon fund. The amount from Watson totalled £500 at the end of 1937.<sup>547</sup> Watson also gave Haldane an additional £200 in 1938 to cover the four month period in which the RF did not fund his work, as discussed in Chapter Two (section 2.2.4).

The amount of recurrent funding Haldane received appears to have risen from approximately £400 plus Haldane's salary at the start of 1937 to £700 plus Haldane's salary at the end of 1937. The amount of funding he received from the RF (£600 p.a.) remained constant, except for a four month period, when he received the equivalent amount from Watson. The section's recurrent funding increased by approximately 30% during 1937. This increase does not appear to be reflected in the type of work the group undertook or the organisms the

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<sup>542</sup> Haldane to Miller, 19 November 1937, b26, Haldane papers, UCL.

<sup>543</sup> Tisdale's diary, May 16 1935, f578, b45, s401D, RG1.1, RFA.

<sup>544</sup> Tisdale's diary, October 21 and 22, 1935, f578, b45, s401D, RG1.1, RFA.

<sup>545</sup> Haldane to Miller, 19 November 1937, f579, b45, s401D, RG1.1, RFA.

<sup>546</sup> Haldane to Miller, 19 November 1937, b26, Haldane papers, UCL.

<sup>547</sup> Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL.

researchers used. The group continued to focus on *Drosophila* population genetics. The additional money appears to have gone to making the group more productive by employing a secretary.<sup>548</sup> It was also used to increase Grüneberg's salary to retain him and to pay a grant to Helen Spurway to retain her.<sup>549</sup> Recurrent funding was sought to stabilise the group. As shown in Chapter Two (section 2.2.5) the group underwent large staff changes during 1936 and 1937. When the recurrent funding increased Haldane therefore used it to increase the group's productivity and to ensure that he retained his staff.

### 3.3.1.3 Individual funding I: 1935-1940

Though the RF took over funding Gordon for a year in 1935 and Grüneberg and Philip from 1936, individuals in the department continued to hold personal grants throughout the period under study. In this section I show that the aims of these bodies were broadly aligned with those of the RF, the university, Haldane and Watson. They therefore appear to have had little influence over the direction of the research. One result, however, was to allow Grüneberg to continue research into developmental genetics, while the rest of the group worked as a collaborative unit, as the RF desired, on population studies.

The major sponsor of individual geneticists at the Department from 1935 was the Royal Society (RS). The RS offered grants to Gordon and Minns in 1935 that enabled them to continue their research on population genetics and mating preferences.<sup>550</sup> In 1938 the RS also awarded funding to Grüneberg, which he retained from October 1938 to October 1942, when he joined the military. The grant paid him a salary of £350 p.a., which was £50 higher than the salary offered by Haldane, and covered his research expenses.<sup>551</sup> This was probably of great importance to Grüneberg since he reported that he was finding it difficult to

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<sup>548</sup> Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL. See also Tisdale's diary, June 22-26, 1937, f579, b45, s401D, RG1.1, RFA.

<sup>549</sup> Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL. Spurway began work in 1936, so it is likely that this makes up the remaining £50 (£150 for a secretary, £50 for Grüneberg, £50 for Spurway, leaving £50 of the £300 spare as stated in the letter).

<sup>550</sup> Tisdale's diary, October 21 and 22, 1935, f578, b45, s401D, RG1.1, RFA.

<sup>551</sup> Davies to Grüneberg, 17 June 1938, folder Roy(3), b14, Grüneberg papers. For a comparison with Haldane's rate of paying Grüneberg, see Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL.

live on the £250 p.a. Haldane paid him in April 1937.<sup>552</sup> This was probably due to the birth of his first child in 1936.<sup>553</sup>

As well as relieving Grüneberg's personal circumstances, the grant ensured Grüneberg's ability to continue developmental research. Grüneberg applied for the funding in the period when the RF's support for the Department had ceased.<sup>554</sup> Grüneberg's future had looked uncertain when he applied for the money, although the Foundation's funding had been renewed by the time Grüneberg was informed of his success in obtaining the grant.<sup>555</sup>

The Royal Society was not the only body to provide the department with individual grants. In 1937 James Rendel joined the department with a small private grant,<sup>556</sup> where he worked on the genetics of *Drosophila sub-obscura*.<sup>557</sup> Nothing further is known of the source of his funding. The Society for the Protection of Science and Learning also supported the Czech refugee, Hans Kalmus, from 1940.<sup>558</sup> He researched the physiology of mutants.<sup>559</sup>

Finally, the RF also supported the work of individuals in the department through its fellowship scheme. Though none of the department's geneticists could obtain one because they did not have permanent positions, Fellows from elsewhere visited the group. In 1936 the Foundation supported L. Csik's visit to UCL, where he worked with Haldane and Fisher on the differential effects of oxygen deprivation within and between species of *Drosophila* for a year.<sup>560</sup> Another

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<sup>552</sup> Miller's diary, April 12, 1937, RG 12.1, RFA. Grüneberg's wage was subsequently raised to £300 by Haldane. (Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL).

<sup>553</sup> Watchorn to Gruneberg, 9 October 1936, folder Wae-Way, b17, Grüneberg papers.

<sup>554</sup> Grüneberg's application was acknowledged on 25 March 1938 (Davies to Grüneberg, 25 March 1938, folder Roy(3), b14, Grüneberg papers). The Rockefeller's grant for 1937/38 ended on 15 February 1938 (Tisdale's diary, November 29-30 and December 1, 1937, f579, b45, s401D, RG1.1, RFA) and the next grant was not approved until April 1938 (Grant-in-Aid 38035, f578, b45, s401D, RG1.1, RFA).

<sup>555</sup> Grüneberg was informed of his success in June 1938 (Davies to Grüneberg, 17 June 1938, folder Roy(3), b14, Grüneberg papers). As per the previous footnote the Rockefeller renewed their grant in April 1938.

<sup>556</sup> Haldane to Weaver, 29 October 1940, f580, b45, s401D, RG1.1, RFA.

<sup>557</sup> Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL.

<sup>558</sup> Haldane to Weaver, 29 October 1940, f580, b45, s401D, RG1.1, RFA.

<sup>559</sup> Haldane to Weaver, 19 June 1940, b26, Haldane papers, UCL.

<sup>560</sup> Miller's diary, November 16-17, 1936, RG 12.1, RFA.



visitor was Sara Bedichek, who came on her own savings to work with Haldane for a year<sup>561</sup> on intersexes of *Drosophila* and lethal genes.<sup>562</sup>

#### 3.3.1.4 The DoZ/B's Funding in Conclusion

Section 3.3.1 shows that there was very little funding for genetics research at a group or departmental level at the DoZ/B. The £1300 the department received from recurrent grants,<sup>563</sup> following the foundation of the DoB, was approximately a quarter of the recurrent grants received by the IAG in 1935.<sup>564</sup> This lack of funding arose from the unplanned manner in which the group grew. It resulted in the group undertaking cheap research: *Drosophila* population genetics. It also resulted in the group being unstable which made it difficult for Haldane to plan the group's research prior to the RF's involvement in 1935.

Most of the funding prior to 1935 came from individual funding, awarded by the Central British Fund for German Jewry, a South African source and the Caisse Nationale. Individual funding continued after the RF began to support genetics activities at the location. The RS, a private source, the Society for the Protection of Science and Learning and the RF itself supported the research of individuals at the department after 1935. The main funding bodies all funded academic research. The RS funded academic science; the RF funded research aimed at understanding life. The Society for the Protection of Science and Learning and the Central British Fund for Germany Jewry did not direct the work of funding recipients but it tended to fund academics. The university, which provided recurrent funding, was also obviously an academic body. The aims of these bodies were therefore all broadly aligned with each other and with Haldane and Watson's visions. The influence of funding bodies on research content is therefore not clearly seen at UCL. The lack of funding influenced the content of the research, however, as Haldane could not conduct expensive research. As discussed above, the RF also affected the group's organisation and planning.

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<sup>561</sup> Miller's diary, June 22, 1937, RG 12.1, RFA.

<sup>562</sup> Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL.

<sup>563</sup> Includes money from the Weldon endowment, the DoZ and the RF. See Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL and Grant-in-Aid 38035, f578, b45, s401D, RG1.1, RFA.

<sup>564</sup> M19, folder Minutes, IAGA.

### **3.3.2 The IAG, Edinburgh**

The funding of genetics research at the IAG was very different from that at the DoZ/B. Almost all the funding was awarded to the location rather than individuals. The location received four types of funding during the 1930s. The first was recurrent funding. With this money the location employed a number of permanent staff. This number never exceeded six or seven during the 1930s.<sup>565</sup> The number of people working at the Institute was always higher than this however because the Institute received project-focused grants. For this sort of research, the Institute hired temporary staff. The Institute also received money from outside bodies to support the work of permanent staff. The other type of funding was capital grants, gifts and donations that were not given for a specific project and were not part of the department's recurrent income. In the following sections I discuss the different types of funding received by the location and how they affected the composition of the Institute.

#### **3.3.2.1 Project-focused funding: Macaulay and the Sex Physiologists**

At the end of the 1920s the President of the Sun Life Assurance Company of Canada, Mr. T.B. Macaulay, became a major sponsor of the Institute. As I show in this section his project-focused funding skewed the IAG's research towards sex physiology. Macaulay's funding gradually declined during the depression, however, resulting in a reduction in the IAG's size and a change in its research focus.

In 1929 Macaulay set up a Trust Fund which provided the department with an annual income to support research into sex physiology.<sup>566</sup> Macaulay's motivation for providing funding appears to be his interest, as an elderly gentleman, in preventing problems relating to senility. The terms of the Trust Deed included:

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<sup>565</sup> Annual Report, 1943-1944, folder IAG Annual Reports, IAGA.

<sup>566</sup> M5a, folder Minutes, IAGA.

“The said revenue shall only be available for the remuneration of persons engaged in or employed in connection with research work of such a character that the results or knowledge sought would be applicable not merely to the lower animals but to mankind. ... The hope of the Donor is that a special Research Laboratory or Section may be established within the Department of Animal Genetics to investigate such problems as those connected with the endocrine glands, vitality and senility...”<sup>567</sup>

Macaulay offered an extra £500 in 1929 stating:

“I am very desirous that Dr. Wiesner and his assistants should extend the scope of their investigations, and in particular that they should prosecute researches dealing with the question of senility and allied subjects.”<sup>568</sup>

In 1930/31 the department received £6100 from Macaulay either as new gifts or from the endowments he had created. This compared with an income of £5483 from governmental sources and £1867 from the university.<sup>569</sup> This income only includes that which Macaulay provided to maintain research in the Institute. In 1930/31 he provided an additional £4500 capital for buildings.<sup>570</sup> The sex physiology section thus brought in 45% of the department’s income in 1930/31.<sup>571</sup> This supports Crew’s recollection that the sex physiology section began to take over the department in the early 1930s.<sup>572</sup>

By 1932 the depression had resulted in the income from Macaulay dropping to £3480 p.a.<sup>573</sup> In 1933 Macaulay provided \$250 a month to keep the sex physiology work going<sup>574</sup> but he could not keep up such payments.<sup>575</sup> This

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<sup>567</sup> M5a, folder Minutes, IAGA. See also Miller’s diary, April 28, 1933, RG 12.1, RFA.

<sup>568</sup> M5a, folder Minutes, IAGA.

<sup>569</sup> A8, folder Memos, financial reports, IAGA.

<sup>570</sup> M5a, folder Minutes, IAGA shows that the income from Macaulay’s first endowment was £1100 p.a. M8, folder Minutes, IAGA shows that income from Macaulay’s second endowment was £2000 p.a. and he gave £3000 p.a. as a gift for three years from 1930. This adds up to £6100 p.a. In addition M8 shows that Macaulay provided £3000 for buildings for the section and £1500 for a rat house. Interview with Crew, CD 7, IAGA shows that it was Wiesner who worked with rats in the department.

<sup>571</sup> Though the figures do not quite match, M8, folder Minutes, IAGA show that all this income from Macaulay was for the sex physiology section. The Minutes suggest that the income from Macaulay in 1930/31 was £9500.

<sup>572</sup> Interview with Crew, CD 7, IAGA.

<sup>573</sup> A8, folder Memos, financial reports, IAGA.

<sup>574</sup> Miller’s diary, April 28, 1933, RG 12.1, RFA.

resulted in all the members of the sex physiology group leaving the location by October 1935.<sup>576</sup>

The income offered by this private individual therefore skewed the balance of the department towards sex physiology in the early 1930s. When the funding failed the shape of the department changed again as the sex physiologists gradually left.

### 3.3.2.2 Project-focused funding: Agricultural Projects

The rest of the project-focused grants the location received during the 1930s were to conduct agricultural genetics projects. Such funding remained reasonably constant throughout the decade, dropping slightly in 1933 and 1935. As I show in this section, such funding maintained breeding genetics activities at the location. Changes in the grants received led to staff changes and different organisms being used for the research. Since the content of this type of research depended on the organism used, content changes also resulted from grant alterations.

The Institute received funding to conduct research into rabbits throughout the decade from the Department of Agriculture. In 1931 the amount the department received for this research was £530.<sup>577</sup> James Pickard came to the Institute to conduct the research at the end of the 1920s.<sup>578</sup> In 1934 the department applied for the grant to be renewed. It seems likely it was since Pickard remained in the department until the end of the 1930s.<sup>579</sup>

From 1928 until 1933 the Empire Marketing Board gave the Institute £800 p.a. to conduct research into sheep.<sup>580</sup> Though the grant from the Empire Marketing Board terminated in 1933, the ARC awarded the Institute £103 for the end of

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<sup>575</sup> M17, folder Minutes, IAGA.

<sup>576</sup> Anonymous to Sir Thomas, 10 October 1935, folder IAG Annual Reports, IAGA.

<sup>577</sup> M10b, folder Minutes, IAGA.

<sup>578</sup> Crew remembers this as having been in 1928. (Interview with Crew, CD 7, IAGA.) It seems more likely it was in 1929, since Pickard reported on his work over the last five years in July 1934. (M17, folder Minutes, IAGA.)

<sup>579</sup> M23a and M23b, folder Minutes, IAGA.

<sup>580</sup> M6, folder Minutes, IAGA. Though the minutes suggest that the amount may be increased, this did not happen as shown by M10, folder Minutes, IAGA.

1933,<sup>581</sup> £101 for January to March 1934 and £600 for 1934/35 to keep the sheep research going.<sup>582</sup> At the start of 1935 W.C. Miller, who had conducted the research alone for the last two years of the project, began a new job in London and the project came to an end.<sup>583</sup>

As this agricultural project came to an end another began, however, although it was slightly less lucrative. From 1935 to 1939 the Scottish Milk Marketing Board made an annual contribution<sup>584</sup> towards work on dairy cattle.<sup>585</sup> For the first year this was £250<sup>586</sup>, but it reduced to £200 p.a from then on.<sup>587</sup> In 1940, however, this amount rose to £800.<sup>588</sup>

One other agricultural project also arose towards the end of the decade. The department received a special grant to research the growth rate of chickens in 1938.<sup>589</sup>

While the amount of money received for breeding genetics projects remained fairly constant through the decade, the organism focused on changed from sheep to cattle around 1935 due to the difficulty in maintaining support for the sheep research and Miller's departure. Staff changes accompanied changes in project-focused grants. For example, Galpin was employed to conduct the research into the growth rate of chickens.<sup>590</sup> The specific content of the work also changed. The sheep research looked specifically at the inheritance of wool in sheep.<sup>591</sup> Though studies on the inheritance of fur in rabbits continued after the sheep research had ended, this was thought of as totally separate research. Thus, while all the research conducted under these grants were breeding genetics activities, the specifics altered.

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<sup>581</sup> M16, folder Minutes, IAGA.

<sup>582</sup> M17, folder Minutes, IAGA.

<sup>583</sup> M18, folder Minutes, IAGA.

<sup>584</sup> F2, folder Minutes, IAGA.

<sup>585</sup> M23, folder Minutes, IAGA.

<sup>586</sup> F1, folder Minutes, IAGA and M20, folder Minutes, IAGA.

<sup>587</sup> A9, folder Memos, financial reports, IAGA. M23, folder Minutes, IAGA.

<sup>588</sup> Annual Report, 1940-1941, folder IAG Annual Reports, IAGA.

<sup>589</sup> M23a, folder Minutes, IAGA.

<sup>590</sup> M23a, folder Minutes, IAGA.

<sup>591</sup> M13, folder Minutes, IAGA.

### 3.3.2.3 Recurrent Funding

During the 1930s the Institute received recurrent grants from the Department of Agriculture for Scotland, the DC/ARC and the University Court for the general maintenance of the location. In this section I show that the ARC had a large influence on the Institute's research, through its control of the type of permanent staff employed there. However, the power over the Institute's direction did not solely reside in the ARC. As I show, the actions of the ARC led Crew to redirect the Institute away from breeding genetics activities, by seeking alternative forms of funding.

In 1931 the ARC was formed to advise the DC and Government agricultural departments such as the Department of Agriculture for Scotland about their support of agricultural research. The Council was mainly made up of highly respected scientists, whose job was to consider the needs of agricultural research and the sciences that underlay it. The role of the Council was therefore to promote science that would aid agriculture, whether that science was pure or applied.<sup>592</sup> On its formation, the Council began to review all the agricultural research occurring in Britain.<sup>593</sup> In October 1932 a sub-committee of the ARC visited the IAG. They concluded:

“It is difficult to avoid the suspicion that the staff of the Institute does not contain sufficient men of real ability to direct so diverse a series of experiments as that which it has undertaken.”<sup>594</sup>

No immediate action was taken while the Council assessed the situation further,<sup>595</sup> other than withdrawing support for Greenwood.<sup>596</sup> In 1935 the ARC

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<sup>592</sup> DeJager, 1993, 138-139.

<sup>593</sup> Cooke, 1981, 23, 25.

<sup>594</sup> A8, folder Memos, financial reports, IAGA.

<sup>595</sup> Miller's diary, April 28, 1933, RG 12.1, RFA shows that the ARC continued to assess the situation. It states that the ARC/DC ceased funding the department while it did so. This seems highly unlikely. The British Treasury agreed to contribute two thirds of the department's expenditure annually in 1926 (Ewing to Hutchison, 16 December 1926, f570, b40, s2, IEBA.) When asked if this had occurred in 1938 Crew stated that it had, except during the depression years when the sum dropped from the agreed £5600 to £5100 (Tisdale's diary, April 30, 1938, f44, b4, s405D, RG1.1, RFA).

<sup>596</sup> Miller's diary, November 17, 1932, RG 12.1, RFA.

again reviewed the work of the Institute and agreed to fund a reduced programme of research. In his diary, the head of the RF's NS, Warren Weaver, wrote:

“They [the ARC and Crew] have come to terms on the basis of a considerably reduced budget, and an understanding, as C.[rew] puts it, that they expect nothing of him. He is a somewhat frustrated person, claiming at one moment that he is content with the reduced plan, and at the next bursting out with his disappointment.”<sup>597</sup>

The reduced plan was for the department to employ five permanent staff, as discussed in Chapter Two (section 2.3.4): Crew, Greenwood, Koller, Fraser Roberts and Buchanan Smith.<sup>598</sup> This shows the influence the ARC had on the shape of the department and the dependence of the permanent staff on it during the 1930s. The Council's influence went beyond staff members to the research conducted. The specialisms of the staff influenced the content of the research they conducted and the content of projects for which they applied for outside funding.

The action of the ARC also had another unintended effect. It encouraged Crew to re-direct the Institute away from breeding genetics activities and towards academic and medical genetic activities. An official departmental letter dated October 1935 stated:

“Applied genetics, since it can claim little or no encouragement is becoming of relatively little importance, whilst fundamental work in cytogenetics will be strengthened...”<sup>599</sup>

As discussed in Chapter Two (section 2.3.5), following the ARC's action the Institute's research refocused onto cytogenetics.

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<sup>597</sup> Warren Weaver officer's diary, May 11, 1935, RG 12.1, RFA.

<sup>598</sup> Warren Weaver officer's diary, May 11, 1935, RG 12.1, RFA. M19, folder Minutes, IAGA.

<sup>599</sup> Anonymous to Sir Thomas, 10 October 1935, folder IAG Annual Reports, IAGA.

### 3.3.2.4 Additional funding for Permanent Staff

Crew's decision to focus on cytogenetics and medical genetics<sup>600</sup> may have been motivated by two medical grants Greenwood was receiving in 1935. As I show in this section, the Institute could refocus on academic and medical genetics activities because the location's permanent staff received additional support for their work from medical and academic funding bodies.

Medical funding bodies supported a variety of work at the Institute, especially towards the end of the 1930s. From 1933, Greenwood received money from the Medical Research Council to biologically assay hormones for other researchers.<sup>601</sup> The Council was still funding Greenwood to do so in 1940/41.<sup>602</sup> The British Empire Cancer Campaign also awarded Greenwood annual grants from 1935 to supply inbred poultry to cancer researchers.<sup>603</sup> This followed a capital grant from the Campaign for an additional poultry plant in 1935. Crew hoped that this would lead to the Institute supplying other animals.<sup>604</sup> In 1940 it did when the Campaign awarded the department £250 for equipment and £200 for the maintenance of a unit to breed cancer mice.<sup>605</sup> In 1940 the Campaign also funded research into tumour susceptibility in fowl and Koller's cytological work.<sup>606</sup> The Scottish Cancer Control Organisation also funded H.J. Muller's research in 1939.<sup>607</sup>

Academic funding bodies also provided additional funding for the research of permanent staff. The Carnegie Trust provided money for the Institute to purchase equipment throughout the 1930s<sup>608</sup> and in 1940 it also gave an additional £150 to

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<sup>600</sup> Anonymous to Sir Thomas, 10 October 1935, folder IAG Annual Reports, IAGA. Miller's diary, December 6 and 7, 1935, RG 12.1, RFA.

<sup>601</sup> Miller's diary, April 28, 1933, RG 12.1, RFA.

<sup>602</sup> Annual Report, 1940-1941, folder IAG Annual Reports, IAGA. See also Annual Report, 1939-1940, folder IAG Annual Reports, IAGA. Annual Report, 1937-1938, folder IAG Annual Reports, IAGA.

<sup>603</sup> Anonymous to Sir Thomas, 10 October 1935, folder IAG Annual Reports, IAGA. Annual Report, 1935-1936, folder IAG Annual Reports, IAGA. Annual Report, 1937-1938, folder IAG Annual Reports, IAGA.

<sup>604</sup> Anonymous to Sir Thomas, 10 October 1935, folder IAG Annual Reports, IAGA.

<sup>605</sup> Annual Report, 1940-1941, folder IAG Annual Reports, IAGA.

<sup>606</sup> Annual Report, 1940-1941, folder IAG Annual Reports, IAGA.

<sup>607</sup> Annual Report, 1939-1940, folder IAG Annual Reports, IAGA.

<sup>608</sup> A2, folder Memos, financial reports, IAGA.



support Koller's work.<sup>609</sup> Towards the end of the 1930s the RF gave the location money to support H.J. Muller and B.M. Slizynski, as discussed above.

Grants from medical and academic research bodies therefore increased substantially towards the end of the decade when, as shown in Chapter Two (section 2.3.5), cytogenetics dominated the work of the department. These grants all went to permanent members of staff, with just one exception.<sup>610</sup> It was presumably easier to persuade the Animal Breeding Committee to agree to accept additional medical or academic funding for staff already employed than to persuade them to apply for grants, and employ additional staff, for medical or academic research, when the Institute's function was breeding.

Agricultural bodies did not provide any additional funding for the work of permanent staff. Having said this, the research of permanent staff was supported by agricultural bodies through the department's recurrent grants. If the staff wanted more money from the ARC or Department of Agriculture for Scotland the additional expense would have been approved or rejected when the department's recurrent budget was agreed each year.

Additional grants from medical and academic bodies were sought because the ARC reduced their support of the Institute. When they withdrew support from Greenwood in 1932 he obtained two medical grants. When the Council further reduced their support in 1935, these grants helped to motivate other members of staff to find additional funding elsewhere. The result was the Institute's refocus onto cytogenetic activities.

#### **3.3.2.5 Gifts, capital aid and equipment**

The final type of funding the department received was gifts, capital aid and equipment that were not for specific projects, such as that referred to from the Carnegie Trust. In this section I show that most of this funding was provided for

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<sup>609</sup> Annual Report, 1940-1941, folder IAG Annual Reports, IAGA.

<sup>610</sup> This was when the British Empire Cancer Campaign awarded money for research into tumour susceptibility in fowl in 1940/41, which was carried out by Mr. J. Carr. Annual Report, 1940-1941, folder IAG Annual Reports, IAGA.

the Institute's farm. It reduced in amount during the decade, reinforcing Crew's perception that the future of the IAG was not in breeding research.

In 1929 Macaulay provided money so the Institute could purchase a farm and in 1930 and 1932 the DC funded the farm's reconditioning.<sup>611</sup> In 1931 the Development Fund paid for the erection of a byre for forty cows.<sup>612</sup> In 1932 a gift of £250 was given to the department which, combined with £250 the Development Fund gave to match the gift, the Institute used to erect bull-boxes.<sup>613</sup> In 1934 an anonymous donor gave the Institute £250 for a lorry.<sup>614</sup> In 1937-1939 the ARC gave the department funding to stock the piggery with tuberculin tested animals.<sup>615</sup>

Such gifts were all made in relation to the department's farm during the 1930s, with the sole exception of the Carnegie Trust's. This was probably because the farm required such funds, since it had only been purchased at the start of the decade.<sup>616</sup> The work of the Institute was discussed in local papers to a reasonable extent.<sup>617</sup> Since farms offer easy access to the work of such Institutes it is highly likely that the purchase of a farm and the need to stock it were discussed in the local papers. In this case, the need for such funding would have been known in the local community. If so, it also explains why most of this type of funding was given at the start of the 1930s, when the purchase of the farm would have been news.

Though this pattern of funding resulted from the newness of the farm in the early 1930s and thus its higher visibility at that time, the farm's need for funding did not reduce during the decade.<sup>618</sup> The reduction in gifts, capital aid and equipment it received therefore only served to reinforce the feeling that agriculturalists were

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<sup>611</sup> A2, folder Memos, financial reports, IAGA.

<sup>612</sup> M9, folder Minutes, IAGA.

<sup>613</sup> M13, folder Minutes, IAGA.

<sup>614</sup> M17, folder Minutes, IAGA.

<sup>615</sup> Annual Report, 1937-1938, folder IAG Annual Reports, IAGA. Annual Report, 1938-1939, folder IAG Annual Reports, IAGA.

<sup>616</sup> "I. M." to Jones, May 1, 1931, f44, b4, s405D, RG1.1, RFA notes that Crew needs £20,000 worth of equipment for the farm, £1000 p.a. for the veterinary physiology section and £1000 p.a. for the human biology section.

<sup>617</sup> See folder IAG Press Cuttings, IAGA.

<sup>618</sup> F1, folder Minutes, IAGA.

not interested in the Institute's work from the mid 1930s, which led the Institute's research away from breeding.

### **3.3.2.6 The IAG's Funding in Conclusion**

In summary, the funding received by the IAG was of four main types: recurrent funding, project-focused funding, additional funding for the work of permanent staff and capital grants and gifts. Different types of bodies provided the different types of funding. For example, agricultural bodies provided all types except additional funding for permanent members of staff. Medical and academic bodies mainly provided additional funding for permanent members of staff.

The types of funding and thus bodies providing it varied throughout the decade. Capital grants and gifts were mainly received at the start of the decade. The project-focused grants Macaulay offered for sex physiological research were also received in the early 1930s. Medical and academic funds for special projects by permanent members of staff were mainly received at the end of the decade. Agricultural recurrent grants and project-focused grants ran throughout. The focus of the IAG correlates well with the types of grants it received throughout the decade.

Though many funding bodies supported the location the ARC had significant control over the location's work and staff as shown by its actions in 1935. The reaction of Greenwood and Crew in finding other sources of funding shows that the research and direction of the Institute was not solely controlled by funding bodies however but also by the staff themselves.

### **3.3.3 Funding Bodies: In Conclusion**

The funding situations at UCL and Edinburgh show a number of differences. Firstly, the scale of funding at the two locations. In 1935 Edinburgh received just over four times the amount of recurrent funding UCL received in 1938.<sup>619</sup> In

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<sup>619</sup> Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL and Grant-in-Aid 38035, f578, b45, s401D, RG1.1, RFA. M19, folder Minutes, IAGA.

1935 the recurrent funding was intended to support five permanent members of staff at the IAG.<sup>620</sup> In 1938 the recurrent funding supported three members of research staff at the DoB.<sup>621</sup> Taking this into consideration the amount of recurrent funding per researcher at Edinburgh was two and a half times as much at UCL. This difference allowed the geneticists at the IAG to undertake more expensive research on agricultural animals and cytogenetic work on a large scale, as Muller did.<sup>622</sup> The work at the DoZ/B however was restricted to inexpensive organisms such as *Drosophila* and mice.

Another difference between the locations was that most of the funding at the IAG was made to the location rather than to an individual. At the DoZ/B this meant that the staff were self-selected to a large extent. Haldane could not advertise for staff because he had no funding to offer. This made it hard for him to redirect his group's research, and thus plan new projects. The lack of permanent funding also made the group unstable, as any of the researchers may have found more permanent funding at any time. This in turn made it difficult for Haldane to plan their research. At Edinburgh the location could advertise and select its staff because the project-focused funding went through the department. This occurred for example, when T.B. Macaulay gave the department money for a Research Fellow in 1930. Crew nominated E. Gabritchevsky for the position and his appointment was approved by the Animal Breeding Research Committee who administered the department.<sup>623</sup>

While the location had more control over the specific staff who worked at Edinburgh, they arguably had less control over the work done. The ARC agreed the positions for permanent staff with the location in 1935. Applications for grants also had to be approved by the Animal Breeding Committee.<sup>624</sup> Haldane, on the other hand, managed to direct the work of his group towards his vision of

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<sup>620</sup> Weaver's diary, May 11, 1935, RG 12.1, RFA. M19, folder Minutes, IAGA. Crew's wage is not included as this came from the endowment for his Chair.

<sup>621</sup> Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL. Haldane's salary, like Crew's is not included, as it came from a separate endowment fund.

<sup>622</sup> Koller to Demerec, 20 December 1939, folder Koller, Peo C #1, Demerec papers.

<sup>623</sup> M8, folder Minutes, IAGA.

<sup>624</sup> See, for example, the approval to apply for support for the pig research in M22, folder Minutes, IAGA.

genetics prior to 1935 and was encouraged to plan his group's work by the RF from 1935. None of the bodies funding the work at the DoZ/B tried to direct its specific content, although as we saw in an earlier section, the RF tried to influence the qualities of the research.

The DoZ/B and the IAG also differed in the type and number of bodies that funded them. Whereas the DoZ/B received its funding from seven different bodies,<sup>625</sup> the IAG received funding from thirteen different bodies during the decade.<sup>626</sup> Haldane's group, as discussed above, was dependent upon the RF's support by 1937. Though the large number of bodies supporting the IAG may suggest that they were not dependent upon any one body, the action of the ARC in 1935 reveals a hidden level of dependency. The location reacted to the control the Council tried to take over the location, however, by seeking out alternative means of support.

The bodies that funded the Institute were far more diverse than those that supported the DoZ/B. At the latter all the bodies were academic and so were all the genetics activities undertaken. At the IAG breeding, medical and academic bodies all offered support. As the balance of the support they offered changed, so did the balance of activities undertaken at the Institute.

### **3.4 Funding at Other British Locations for Genetics**

In this section I consider the types of bodies that funded genetics at other major British locations for genetics during the 1930s. This demonstrates that the funding situations at Edinburgh and UCL were reasonably representative of their respective settings.

#### **3.4.1 The Funding of Genetics at Academic Locations**

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<sup>625</sup> University College London (whether the Weldon endowment or the DoZ), the Central British Fund for German Jewry (later the Society for the Protection of Science and Learning), a South African source, the Caisse Nationale, the RF, the Royal Society and a private source.

<sup>626</sup> Empire Marketing Board, Milk Marketing Board, DC, ARC, Department of Agriculture for Scotland, British Empire Cancer Campaign, Medical Research Council, Scottish Cancer Control Organisation, the University Court, the Carnegie Trust, the RF, T.B. Macaulay and an anonymous donor.

In this section I show that there was very little funding for genetics within the academic setting. Recurrent funding all came from universities. This tended to support a minimal amount of academic genetics activity as part of either zoology or botany programmes. The RF only offered funding for animal genetics, which excluded botany departments from their clientele. As seen for UCL, the RF's funding tended to complement the universities' influence over the locations, directing the work towards broad, academic programmes. The major differences within the setting were that the RF did not support genetics in botany departments and that botany departments found it easier to obtain government funding.

All the locations in the academic setting received their recurrent funding from a university. However, the type of bodies that additionally supported genetics at academic locations depended on whether the department was directed towards the study of botany or zoology. Botany departments such as that at Manchester obtained funding from governmental sources. In 1937, for example, the head of the Manchester department, Montagu Drummond, attempted to collect funds to get a Ministry of Agriculture grant for a Horticultural Station.<sup>627</sup> In obtaining grants, the Manchester department took advantage of the connection between botany and horticulture. In 1936 the department gained a geneticist following a donation of £70,000. This capital could not be touched but the income from it amounted to £2000 p.a. The only conditions were that the department provided two scholarships in practical gardening and gave gardening evening classes.<sup>628</sup> The only zoology department to receive governmental money for genetics was at Aberdeen University. This grant was mainly to fund work on fisheries, but the head of department, Lancelot Hogben, also obtained some governmental money to employ genetics assistants.<sup>629</sup>

Zoology departments had access to Rockefeller aid however. This tended not to be open to botany departments. As Miller told Drummond at Manchester, the

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<sup>627</sup> Miller's diary, October 21, 1937, RG12.1, RFA.

<sup>628</sup> Miller's diary, January 31, 1936, RG12.1, RFA.

<sup>629</sup> Hogben to Tisdale, 12 December 1939, f39, b3, s405D, RG1.1, RFA.

Foundation was far more interested in animal than plant genetics.<sup>630</sup> The RF granted aid to Hogben at Aberdeen to employ a research assistant to help him “in his researches in genetics, population problems, hormones and reproduction physiology...”<sup>631</sup> The RF reinforced the university’s influence, directing academic genetics activities towards being part of a broader zoological programme of research.

Some of the departments appear not to have received funding from outside bodies. One example is the academic location at Cambridge University. Pease received Ministry of Agriculture money for his work with fowl, but he did so as part of the Agricultural Faculty’s Institute of Animal Nutrition, not as Punnett’s assistant.<sup>632</sup> Information on the funding of genetics at other locations is too incomplete to comment upon.

One of the differences noted between the DoZ/B and the IAG was that only the latter received Rockefeller Fellowships. Though none of the geneticists in the academic setting received one during the 1930s, the Foundation expressed strong interest in awarding a fellowship E.B. Ford, who researched genetics at Oxford University.<sup>633</sup> In my opinion, this difference between the two settings had more to do with the lack of geneticists in the setting, or at least in permanent positions in the setting, than Rockefeller policy.

This discussion suggests that the DoZ/B was reasonably representative of funding within its setting. All the major locations in the academic setting (DoZ/B at UCL, Kings College London, Cambridge, Aberdeen, Manchester) received their recurrent maintenance grant from the university and the university alone. None of them received much outside aid. The DoZ/B was more representative of zoology departments, however, which were generally supported by the RF. Botany departments could exploit their connection to horticulture to obtain more applied funding, but the majority of outside funding in this setting was academic.

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<sup>630</sup> Miller’s diary, January 31, 1936, RG12.1, RFA.

<sup>631</sup> Grant-in-Aid 37187, f39, b3, s405D, RG1.1, RFA.

<sup>632</sup> Miller’s diary, October 27, 1937, RG12.1, RFA.

<sup>633</sup> Miller’s diary, November 11, 1932, RG12.1, RFA.

### 3.4.2 The Funding of Genetics at Breeding Locations

In this section I show that the funding of genetics at the IAG was also reasonably representative of the funding in its setting. As discussed in Chapter Two (section 2.5.2), the majority of the locations were supported by the DC/ARC. A number of breeding locations received money from both the Commission and a university: The IAG, the Plant Breeding Institute<sup>634</sup> and the Welsh Plant Breeding Station.<sup>635</sup>

The recurrent funding of the IAG was therefore typical. However, there was diversity in the setting. The recurrent funding of the JI was derived from a legacy in John Innes's Will.<sup>636</sup>

Little information is available on the outside funding received by these locations. However, it should be assumed that it was normal for them to receive outside funding from applied bodies, since matching funds were a condition of DC funding.<sup>637</sup> The JI received some outside funding, mainly from applied bodies. For example, in 1939 three of the research workers there were funded by the Ministry for Agriculture.<sup>638</sup> The Worshipful Company of Fruiterers also gave the Institution £50 p.a. from 1926 for a member of the gardening staff working with fruit.<sup>639</sup> The Institute also received some funding from academic bodies. For example, the cytogeneticist, Cyril Darlington, received funding from the RF in 1938 for cytological equipment.<sup>640</sup> He also received a Rockefeller Fellowship in 1931.<sup>641</sup> However, these awards were not necessarily for genetics work. The RF grant was also for academic genetics activities conducted in a breeding location.

Thus most of the breeding locations received governmental funding from the Ministry of Agriculture, the ARC or the DC. Many received recurrent funding

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<sup>634</sup> Palladino, 2002, 43-44.

<sup>635</sup> Palladino, 2002, 51.

<sup>636</sup> Olby, 1989.

<sup>637</sup> Palladino, 2002, 43.

<sup>638</sup> Darlington to Tisdale, March 29, 1939, f449, b35, s401D, RG1.1, RFA.

<sup>639</sup> The JI Horticultural Institution Record of Work 1910-1935, f449, b35, s401D, RG1.1, RFA.

<sup>640</sup> Grant-in-Aid 38140, f449, b35, s401D, RG1.1, RFA.

<sup>641</sup> Fellowship 31103, Natural Sciences Fellowship Recorder Cards, RFA.



from a university, but none of them received it from a university alone as was common in the academic setting. Outside funding was also a typical feature of the breeding setting, since it was encouraged by the DC. These sources tended to be applied but also included some academic bodies.

### **3.5 Conclusion**

The funding received by genetics locations in 1930s Britain varied with setting. All British locations for genetics in the academic setting received their recurrent funding from a university during the 1930s. The funding served to maintain a Department of Zoology, Botany or more rarely a department of genetics or biometry. The funding given by the university therefore directed the research towards problems that had bearing on one of these academic disciplines. The funding offered by the RF reinforced the influence of the university's funding in zoology departments. The RF tended not to fund botany departments. The RF encouraged experimental academic research with wide applicability, such as genetics research directed towards increasing understanding of zoology. This conjunction of interests explains why the genetics research conducted in the academic setting tended to be of broad applicability.

This Chapter also explains why the academic setting employed so few geneticists during the 1930s. This was due to the lack of funding available to academic locations. Universities provided a minimal amount of funding to include genetics in zoology or botany programmes. Little soft money was available, and so the genetics activity of a department usually remained minimal. Haldane's case shows that the RF was interested in funding the establishment of academic animal genetics programmes, where there was a hierarchical structure and the group worked as a collaborative unit. The RF's interest in the DoZ/B and the IAG arose from the potential for such a programme to develop at each of the locations. Though the RF did not support such a programme at either location, both were running programmes of research at the end of the 1930s. The DoZ/B's derived from the planning the RF encouraged Haldane to do. The IAG's arose

due to Muller's perception of genetics research being closely aligned with the RF's, possibly due to previous RF grants.

These two points add to the understanding of the definition of genetics in Britain. Harwood argued that the position of geneticists in generalist departments in Germany led to a broader definition of genetics than existed in America.<sup>642</sup> My first conclusion argues exactly the same for the British academic setting, although it also points out the RF's role in encouraging a broad definition. Due to the field of genetics generally being considered as a whole the concept of genetics in the breeding setting (generally narrow) has swamped the concept in the academic setting. A better understanding of the definition of genetics in Britain can therefore be gained by considering the settings independently.

Recurrent funding in the breeding setting usually came from the DC/ARC and a university. By only providing recurrent funding to locations in the breeding setting, the DC/ARC recognised the breeding setting as a discrete entity. Through its recurrent funding the ARC encouraged research that would be beneficial for agriculture. This varied from fairly academic research, such as Koller's, on the cytogenetics of the breeding process to more applied research. The latter included A.D. Buchanan Smith's work analysing Shorthorn herds of cattle.<sup>643</sup> The activities encouraged by the ARC, and those conducted in breeding locations, were therefore a mixture of breeding and academic. The structure the ARC encouraged through their recurrent grants was collaborative. Different researchers were supposed to be employed to work on different, but related subjects.

The ARC also offered project-focused grants. These grants were awarded to locations to employ temporary staff to conduct the research. Breeding locations, unlike most academic locations (the DoZ/B being an exception), therefore had temporary staff. Project-focused grants were far more readily available to breeding locations than academic locations. Due to the variety of grants available

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<sup>642</sup> Harwood, 1993, 178.

<sup>643</sup> A8, folder Memos, financial reports, IAGA. Buchanan Smith to Wright, 15 March 1933, folder Buchanan-Smith, A[lick] D, Wright papers.

from medical and breeding funding bodies, breeding locations could take on a variety of shapes. The IAG had more medical and academic research occurring than most breeding locations, while locations such as the Poultry Breeding Centre received few project-focused grants.

The funding of British genetics can therefore be seen to have been divided along the lines of setting. Furthermore, the ARC clearly recognised the boundaries between the breeding setting and the medical and academic settings. It provided locations in the breeding setting with recurrent funding. The RF did not recognise such boundaries because it focused on research function rather than structure. It therefore recognised a boundary the ARC did not: that between academic and breeding activities. Nevertheless, since the boundaries between academic and breeding activities and settings coincided reasonably well, the RF's funding was heavily concentrated in the academic setting.

As well as forwarding my thesis and our understanding of British genetics generally, this Chapter adds to the literature on the RF. Kay<sup>644</sup> argued that the RF had enormous influence over the development of molecular biology. In this Chapter I have shown that this was also true of the RF's influence on genetics in the academic setting. It was one of the only sources of external funding available to geneticists in this setting and it therefore had a great deal of leverage, as seen in Haldane's case. Zallen<sup>645</sup> has argued that the RF used this influence to push American values, such as interdisciplinary work. I have shown that the RF promoted broad, programmatic research. I have also argued that the appearance of pushing American work may have arisen because the RF was heavily dependent upon American scientists to tell them who was worthy of support. This dependence on scientists' opinions has previously been noted by Abir-Am.<sup>646</sup> The RF did not push research content within academic genetics activities, and this gave rise to the type of dialogues Kohler<sup>647</sup> has noted.

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<sup>644</sup> Kay, 1993.

<sup>645</sup> Zallen, 1989.

<sup>646</sup> Abir-Am, 1982.

<sup>647</sup> Kohler, 1991a.

## **Chapter Four**

### **Research Organisms**

#### **4.1 Introduction**

In this chapter I study another characteristic of genetics: research organism. I establish the different organisms used at the DoZ/B and the IAG and consider whether differences between the locations were representative of those between the locations' respective settings. I then investigate whether or not mice were used as research tools at the two locations.

I begin, in section 4.2, by investigating the diversity of organisms used at each location. A far wider range of organisms were used at the IAG than the DoZ/B. Organisms at the IAG tended to be agricultural, but also included pedigree animals, laboratory animals, and miscellany. Organisms at the DoZ/B were almost all laboratory animals, although these varied enormously in the amount of genetic manipulation they had undergone.

Next, in section 4.3, I investigate how representative the differences between the DoZ/B and the IAG were of the differences between the academic and breeding settings. I show that in the British academic setting the animals used tended to be small, inexpensive and often, wild. Few animals were studied at any one location and they rarely had commercial value. The plants studied tended to be horticultural. This was possibly because, as seen in Chapter Three (section 3.4.1), botany departments often exploited their links to horticulture to obtain additional funding. In the breeding setting the organisms used tended to be horticultural or agricultural. With the exception of those used at the IAG, they tended to be plants. All the organisms were therefore large, expensive, and domesticated. The number of organisms studied varied between the locations, but all had commercial value.

Finally, in section 4.4, I study whether mice were treated as research tools at the two locations. I show that they were treated as tools at the DoZ/B, which could

be used to investigate problems which extended beyond the genetics of mice. I show that mice were not considered to be tools at the IAG but live organisms of interest themselves.

## **4.2 Types and Uses of Organisms**

In this section I compare the types of organisms at the DoZ/B and the IAG and how they were used. Both locations used a variety of different types of organisms in their work. During the decade wild organisms were increasingly preferred at the DoZ/B, while the main focus at research at the IAG was domesticated organisms. At the DoZ/B animals tended to be used as models for generic ‘organisms’, while this usage of animals was strongly resisted at the IAG until the end of the decade.

### **4.2.1 Analytic Framework**

#### **4.2.1.1 Types of Organism**

I distinguish between three types of organism: artificial, domesticated and wild. Artificial organisms were those whose genetic composition had been designed. For example, Grüneberg designed the genetics of the mice he used in linkage experiments so that they had two recessive alleles in coupling and one in repulsion.<sup>648</sup> This enabled him to tell how much crossing-over occurred when these mice were crossed with inbred mice. Inbred mice were also artificial as they were designed to be homozygous at every gene loci.

Domesticated organisms were those whose physical and/or behavioural characteristics had been designed. These included laboratory animals, farm animals, pedigree animals, agricultural plants and horticultural plants. Laboratory animals had been bred to be tame, and had often been selected for traits such as high or low cancer rates. Farm animals and agricultural plants were bred for high

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<sup>648</sup> Alleles on the same chromosome in a homologous pair are in ‘coupling’; alleles on different chromosomes in a homologous pair are in ‘repulsion’.

yield. Pedigree animals and horticultural plants were bred for certain show characteristics.

Wild animals were those that existed in the wild; whose genetic and physical characters had not been purposefully influenced by man.

#### 4.2.1.2 Uses of Organisms

Any group of physical objects sharing an identity can be modelled by any one member of the group. For example, the group 'mice' can be modelled by any mouse. A mouse can also model the group 'mammals' or 'organisms' as it also belongs to both these groups. The physical object that forms such a model, in this case a mouse, is here termed a 'physical model'. As suggested above, the group being modelled can vary in size, in this case from a type of organism (mice) to organisms in general. These groups form an is-a hierarchy. For example, mouse is a mouse, is a mammal, is a vertebrate, is an organism.<sup>649</sup> In all the cases studied below, organisms were used as physical models. The results were always claimed to hold for a group of organisms, rather than only for the specific organisms used in the research. In section 4.2, I identify how far researchers at the DoZ/B and the IAG tended to move up the is-a hierarchy. I show that researchers at the DoZ/B typically used organisms as a physical model for 'organisms'.<sup>650</sup> At the IAG researchers usually remained further down the is-a hierarchy.

I also investigate the epistemological caution of the researchers at each location. I distinguish between the use of a physical model of 'organisms' and the use of a physical model as an instance of 'organisms'. The former only required one type of organism to be used as a model of 'organisms'. This was common at the DoZ/B. The latter required several types of organism, for example mice, rats and

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<sup>649</sup> The type group 'mouse' is low down the is-a hierarchy, the type group 'organism' is high up the hierarchy.

<sup>650</sup> By 'organisms' I mean the type group to which all organisms belong and no non-organisms belong. Physical models for 'organisms' are generally termed 'model organisms' in the literature. See for example, Creager, 2002, 4-5.

dogs, to be studied before generalisations could be made about ‘organisms’. This was common at the IAG.

#### **4.2.2 Organisms used at the DoZ/B**

In this section I investigate the different organisms used at the DoZ/B for research. I show that as the balance between the types of organisms used for research altered, so did the balance between the research areas studied. Wild animals were increasingly used at the location in preference to artificial and domesticated animals. This finding is contrary to expectation. Löwy and Gaudillière have noted that by shipping inbred mice out to other laboratories, the Jackson Laboratory promoted “a shared culture of standardization.”<sup>651</sup> Haldane was credited in part with the success of the Jackson Laboratory and promoted the use of inbred mice, as discussed below.<sup>652</sup> However, by their increasing use of wild organisms, Haldane’s genetics group did not participate in the “shared culture of standardisation.” I also show that the predominant use of organisms was as physical models for ‘organisms’. The geneticists at the DoZ/B therefore tended to move a long way up the is-a hierarchy.

##### **4.2.2.1 Mice**

Mice were a major research organism at the DoZ/B. The major value of using them for research came from their standardisation. As the department moved towards using wild animals, mice lost their value. They were therefore used less for research as the decade advanced.

As discussed in Chapter Two (section 2.2.2), when Haldane joined the DoZ he planned to conduct a variety of physiology, pharmacology and linkage experiments with different strains of mice. He brought a variety of different

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<sup>651</sup> Löwy and Gaudillière, 1998, 225.

<sup>652</sup> Weaver’s diary, August 20, 1934, RG12.1, RFA.

mouse strains<sup>653</sup> back from America in 1932 and acquired others from elsewhere.<sup>654</sup>

By the end of 1934 mice were used in the Department to research all the subjects Haldane had earlier planned, except pharmacological differences. They were used to compare serological differences between strains by Gorer,<sup>655</sup> to perform linkage tests by Grüneberg<sup>656</sup> and to study the physiological differences between strains by Pierre Lafon.<sup>657</sup> Gorer and Lafon used mice as models of ‘organisms’,<sup>658</sup> while Grüneberg used the mice as models of generic ‘mice’. In late 1934 a developmental mutation arose in one of the department’s mouse stocks. The availability of this mutation led to developmental genetics being studied with laboratory mice in the department.<sup>659</sup> These mice were used as an instance of ‘organisms’, as discussed in section 4.4.2.3. Artificial mice were used for all this work as, with the exception of Grüneberg’s study, they were all inbred. Grüneberg designed the genetics of the mice he studied, so he could investigate the linkage of the developmental mutation.

As the decade advanced the amount of mouse genetics in the department decreased. Lafon left the department in 1935 at the end of his year’s visit. Gorer began work at the Lister Institute part time in 1934.<sup>660</sup> The amount of work he performed with mice at UCL decreased thereafter, before ending in 1936. However, Grüneberg’s work on the developmental genetics of mice continued. As seen in Chapter Five (section 5.2.1), this work was slightly incongruous in the department. It continued mainly because Grüneberg remained at the department throughout the decade. By the time he finished researching the original mutation, he was highly trained in this type of work, which could only be done with artificial or domesticated animals.

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<sup>653</sup> All the mice used in the department during the 1930s appear to have been *Mus musculus*, or house mice.

<sup>654</sup> Haldane to Dunn, November 9, [1932], folder Haldane, J.B.S., Dunn papers. Haldane to Dunn, July [1933], folder Haldane, J.B.S., Dunn papers.

<sup>655</sup> Miller’s diary, March 14-15, 1934, RG12.1, RFA.

<sup>656</sup> Miller’s diary, March 14-15, 1934, RG12.1, RFA. Grüneberg, 1935a. Grüneberg, 1936a.

<sup>657</sup> Miller’s diary, October 22, 1934, RG12.1, RFA.

<sup>658</sup> For further details of Gorer’s work see section 4.4.2.2.

<sup>659</sup> Miller’s diary, October 22, 1934, RG12.1, RFA. Grüneberg, 1935c.

<sup>660</sup> Medawar, 1961, 97.



In the middle of the decade a few isolated pieces of mouse research were performed using wild mice. In 1935 Philip searched for recessive genes in wild populations of mice and tried to explain their frequency with reference to the size of the breeding population.<sup>661</sup> Philip's research compared the population genetics of mice and the beetle, *Dermestes*. The mouse and *Dermestes* populations therefore acted as instances rather than models of 'organism' populations.

The work on haemoglobin differences, which Lafon had performed at the Department, also appears to have been extended to a comparison of laboratory and wild mice at this time.<sup>662</sup> This work tested the limits of inbred mice as a physical model for 'mice'. The findings of the work reportedly caused Haldane to develop an interest in the effects of domestication at this time.<sup>663</sup> The difference between wild and laboratory animals has been discussed by historians such as Kohler, who has suggested that the latter were constructed technologies.<sup>664</sup> This idea has been followed up by others. Logan concluded from her study of laboratory Norway rats that they were standardised experimental tools but due to the changes they went through to become standardised it was questionable whether they were still Norway rats.<sup>665</sup> There is therefore a tension between standardisation and the sufficiency of laboratory animals to act as physical models. The results of Lafon's work appear to have led Haldane to question the sufficiency of laboratory animals as physical models. This may be one of the motivations behind the department's transition to using wild organisms for research. Evidence for other causes has not been identified in the course of my research.

During the decade mice were used as instances or models of 'organisms' to research the genetics of physiological and developmental processes at the DoZ/B. Such processes were relatively easy to study in mice but not in *Drosophila*, which were the other favoured organism of the department. Mice

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<sup>661</sup> "Work in progress in de [sic] department of genetics University College, London", f578, b45, s401D, RG1.1, RFA. Philip, 1938.

<sup>662</sup> Miller's diary, November 16-17, 1936, RG12.1, RFA.

<sup>663</sup> Miller's diary, November 16-17, 1936, RG12.1, RFA.

<sup>664</sup> Kohler, 1994.

<sup>665</sup> Logan, 2001, 309-310.

were also relatively small and inexpensive, in comparison to other organisms such as dogs (discussed later). The suitability of mice for physiological genetics originates partly from their standardisation. As the department moved towards using wild organisms the focus of research at the DoZ/B changed from physiological to population genetics. Simultaneously, the amount of research conducted with mice decreased.

#### 4.2.2.2 *Drosophila*

The other major organism used at the DoZ/B was *Drosophila*. In this section I show that, as for mice, the use of artificial *Drosophila* decreased during the decade as the use of wild *Drosophila* increased. Though Haldane appears to have questioned the suitability of artificial animals as models for generic ‘organisms’, he does not appear to have questioned the ability of organisms to act as models for ‘organisms’ in principle. Thus, the wild *Drosophila*, like the artificial animals, were used as models of ‘organisms’.

Artificial, laboratory *Drosophila melanogaster* were used in the department because they had well defined genetics. Their chromosomes were well mapped and so they were useful tools for chromosomal genetics research. Much of the work done with *D. melanogaster* was chromosomal genetics. For example, Grüneberg used *D. melanogaster* to investigate a chromosomal inversion and re-inversion by seeing how the gene map changed.<sup>666</sup> The inversions were also studied cytologically.<sup>667</sup> From this research Grüneberg drew conclusions about the reality of position effects in ‘organisms’. The flies were therefore used as models of ‘organisms’. *D. melanogaster* was one of the species Philip used at that time for chromosomal genetics too. She studied crossing-over in the sex chromosomes.<sup>668</sup> Her work was intended to reveal how heterogeneity was maintained in the sex chromosomes of organisms in general rather than specifically in *Drosophila*. Her work therefore also used *D. melanogaster* as models of ‘organisms’. A.L.M. Christie studied the linkage groups of lethal

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<sup>666</sup> Grüneberg, 1935b.

<sup>667</sup> Koller, 1935b.

<sup>668</sup> Philip, 1935.

mutations caused by X-rays in laboratory *D. melanogaster*.<sup>669</sup> His work was intended to compare the chromosomes of different species of *Drosophila* to provide information about evolution in general. Thus, while his work used his *D. melanogaster* stocks as a physical model of '*D. melanogaster*', the long term aim of the research was for it to provide information about organisms in general.

*D. melanogaster* was used for purposes other than chromosomal genetics. Cecil Gordon used wild *D. melanogaster* for population genetics purposes. Gordon investigated how the frequency of a gene released into a wild population changed with time.<sup>670</sup> His populations of *D. melanogaster* acted as models of 'organism' populations. F.C. Minns studied the mating preferences of *D. melanogaster*.<sup>671</sup> Like Christie's research, this used *D. melanogaster* as a physical model of *D. melanogaster*, but was conducted to provide information about evolution in 'organisms' in general. Thus, research with *D. melanogaster* usually used the organisms as models of 'organisms', and even more commonly was done to eventually gain information at this level of the is-a hierarchy.

Work with *D. melanogaster* appears to have ended in 1938. By then Christie, Minns and Gordon had all left the department. Grüneberg was concentrating on developmental genetics with mice and Philip had changed organism to *Dermestes* (see below). Work with *Drosophila* continued but it was mainly population genetics, conducted with other species. The advantage of *D. melanogaster* was its standardisation. Once wild organisms were used, its advantage over other *Drosophila* species was lost.

While research with *D. melanogaster* declined during the decade, work on *Drosophila sub-obscura* increased. Wild *D. sub-obscura* were used in the department as early as 1934, when Gordon compared the population genetics of *D. melanogaster* and *D. sub-obscura*.<sup>672</sup> This study used the two populations as

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<sup>669</sup> Christie, 1939/1940.

<sup>670</sup> Gordon, 1936.

<sup>671</sup> Summary of work in progress, October 3, 1934, f578, b45, s401D, RG 1.1, RFA. Work in Progress in de [sic] Department of Genetics University College, London, f578, b45, RG 1.1, RFA.

<sup>672</sup> Summary of work in progress, October 3, 1934, f578, b45, s401D, RG 1.1, RFA. Gordon, 1936.

instances of populations of ‘organisms’. A year later Gordon’s study of wild *D. sub-obscura* had expanded to include an investigation of gene linkage. This used the *Drosophila* as a model of ‘organisms’. In 1935, Christie switched *Drosophila* species and began working on the biology of *D. sub-obscura* and the effects of X-rays on them.<sup>673</sup> The *D. sub-obscura* Christie worked on were presumably derived from the wild *Drosophila* Gordon worked with, because the species was only studied at UCL<sup>674</sup> and so standardised laboratory *D. sub-obscura* would not have been available. As for *D. melanogaster*, the research used *D. sub-obscura* as a physical model of ‘*D. sub-obscura*’, but was conducted to provide information about evolution in organisms in general. In 1936/37 Gordon and Christie left the department. Work on the genetics of wild *D. sub-obscura* was continued however by Spurway, Street and Rendel.<sup>675</sup> This used *D. sub-obscura* as a model of ‘organisms’. Thus the work with wild *D. sub-obscura* was done to gain information about ‘organisms’. It was commonly used as a model of ‘organisms’ but also as an instance of them.

*D. sub-obscura* was used in the department in preference to *D. melanogaster* for work on population genetics. This requires explanation because the chromosomes of *D. melanogaster* were well mapped, which eased genetic studies. *D. sub-obscura* was preferentially used probably because Haldane believed it was more mutable than *D. melanogaster*<sup>676</sup> and because the Department was the only location researching the species.<sup>677</sup> Research on *D. sub-obscura* was therefore a niche area for the DoZ/B.

Several other *Drosophila* species were also used in the department. In 1934 Philip researched the genetics of an unknown *Drosophila* species, thought to possibly be *Drosophila immigrans*. At the same time Koller was investigating the cytology of *Drosophila pseudo-obscura*.<sup>678</sup> There is little evidence of more work

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<sup>673</sup> Work in Progress in de [sic] Department of Genetics University College, London, f578, b45, RG 1.1, RFA.

<sup>674</sup> Projects for Research in Animal Genetics, f578, b45, s401D, RG1.1, RFA.

<sup>675</sup> Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL. Haldane to Tisdale, 18 December 1937, b26, Haldane papers, UCL. Haldane to Weaver, 22 September 1939, f579, b45, s401D, RG1.1, RFA. Gordon, Spurway and Street, 1939.

<sup>676</sup> Miller’s diary, October 22, 1934, RG12.1, RFA.

<sup>677</sup> Projects for Research in Animal Genetics, f578, b45, s401D, RG1.1, RFA.

<sup>678</sup> Summary of work in progress, 3 October 1934, f578, b45, s401D, RG1.1, RFA.

on *D. pseudo-obscura* at the DoZ/B except that a sex-linked mutation arose in the species during 1937.<sup>679</sup> *D. pseudo-obscura* was therefore presumably kept in the department and used for comparative work. *Drosophila obscura* may have been another such species since Cecil Gordon published a piece on the sex ratio of the species in 1937.<sup>680</sup>

*Drosophila* was a major research organism at the DoZ/B from 1933, but it became more important as the decade advanced. The *Drosophila* used changed from artificial *D. melanogaster* to wild *D. sub-obscura*. As Haldane became concerned about the effects of domestication, he began to perceive the artificial animals as potentially problematic physical models. The organisms his group used therefore changed from artificial to wild. This meant that their genetics had not been influenced by humans, so they were more natural. The group still used *Drosophila* as models of 'organisms' but they became more epistemologically cautious. More comparative work was done, which did not use one species as an isolated model. Philip also began to work with *Dermestes* in the middle of the decade, which Haldane pointed out provided a check on findings made with *Drosophila*.<sup>681</sup>

#### 4.2.2.3 Humans

Mice and *Drosophila* were the organisms of choice at the DoZ/B. However, other organisms were used. Haldane, for example, was interested in the genetics of man. Humans were normally studied as physical models for 'humans'. Since no other organism could be used to model the group 'humans', this explains why their use as a research organism did not decrease during the decade, as a move was made towards wild organisms.

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<sup>679</sup> Miller's diary, April 17-22, 1937, RG12.1, RFA.

<sup>680</sup> Gordon, 1937.

<sup>681</sup> Haldane to Tisdale, 13 December 1937, b26, Haldane papers, UCL.

Between 1934 and 1939 Haldane researched human linkage.<sup>682</sup> Part of this work was carried out in collaboration with the Eugenics Department's geneticist, Julia Bell.<sup>683</sup> In 1935 Haldane also researched the mutation rate of a human gene in collaboration with the Royal Eastern Counties' Institution's geneticist, L. Penrose.<sup>684</sup> In 1935 and 1936 he also investigated the frequency of lethal genes in man.<sup>685</sup> These researches had obvious links to eugenics. Humans were therefore studied as physical models for 'humans'. The research also had links to population genetics, however, as Haldane pointed out in 1937.<sup>686</sup> This meant that the results could also be used as an instance of population genetics.

Haldane was not alone in researching human genetics in the department. Ursula Philip helped Haldane with some of his human genetics studies.<sup>687</sup> Grüneberg also performed some human genetics work independently. When he first entered the department Grüneberg began work on the inheritance of a human disease.<sup>688</sup> For this work humans were used as models for 'humans'.

In one case humans were used differently. In 1936 Grüneberg published an article on a human family who lacked upper canines and wisdom teeth.<sup>689</sup> At the same time, he was studying a pathological mutation in mice that prevented the eruption of their teeth. This research was probably not done because Grüneberg was interested in the genetics of humans in particular. The case formed a good comparison to the research he was then doing in mice. Humans were therefore used as an instance of development in this case.

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<sup>682</sup> Summary of work in progress, 3 October 1934, f578, b45, s401D, RG1.1, RFA. Tisdale's diary, November 21 and 22, 1935, f578, b45, s401D, RG1.1, RFA. Haldane to Tisdale, January 27, 1936, f579, b45, s401D, RG1.1, RFA. Miller's diary, November 16-17, 1936, RG12.1, RFA. Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL. Haldane to Weaver, 3 November 1939, f579, b45, s401D, RG1.1, RFA.

<sup>683</sup> Tisdale's diary, October 21 and 22, 1935, f578, b45, s401D, RG1.1, RFA.

<sup>684</sup> Work in Progress in de [sic] Department of Genetics University College, London, f578, b45, s401D, RG1.1, RFA. Haldane, 1935.

<sup>685</sup> Haldane to Tisdale, 15 February 1936, f579, b45, s401D, RG1.1, RFA. Miller's diary, January 28-29, 1937, RG12.1, RFA.

<sup>686</sup> Haldane to Tisdale, 18 December 1937, b26, Haldane papers, UCL.

<sup>687</sup> Haldane and Philip, 1939.

<sup>688</sup> Grüneberg, 1934.

<sup>689</sup> Grüneberg, 1936c.

#### 4.2.2.4 The Beetle, *Dermestes*

In this section I show how *Dermestes vulpinus* came to be used as the department moved towards using wild organisms for their research. Philip's use of them probably arose from a study she conducted with Grüneberg in 1935 to see how suitable three coleopteran species were for genetic analysis.<sup>690</sup> At the start of 1936 Haldane listed research into the genetics of *Dermestes vulpinus* as one of the department's projects in the last year.<sup>691</sup> By 1937 Philip was not just researching the genetics of *Dermestes vulpinus*, she was also using them for population genetics.<sup>692</sup> Such work continued in the department until Philip evacuated to the John Innes (JI) in September 1939.<sup>693</sup> In the case of the population genetics, the *Dermestes* were wild. Presumably this was also true of the beetles Philip used for transmission genetics. The beetles were used as instances of population genetics. Originally, Philip compared the genetics of populations of *Dermestes* and mice.<sup>694</sup> Later, the research formed an epistemological check on the research conducted with *Drosophila*, which used them as models of 'organisms'.<sup>695</sup>

#### 4.2.2.5 Rats

The rats used at the DoZ/B tended to be artificial. This was because developmental mutations that arose in laboratory rat stocks gave geneticists at the DoZ/B the opportunity to investigate the genetics of development. The genetics of the rats were manipulated to investigate linkages to the developmental mutations. This manipulation made the organisms artificial.

In 1937 Grüneberg began to research developmental genetics with the laboratory rat, *Rattus norvegicus*.<sup>696</sup> An inherited emphysema arose in Grüneberg's rat

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<sup>690</sup> Work in Progress in de [sic] Department of Genetics University College, London, f578, b45, s401D, RG1.1, RFA.

<sup>691</sup> Haldane to Tisdale, 15 February 1936, f579, b45, s401D, RG1.1, RFA.

<sup>692</sup> Miller's diary, April 17-22, 1937, RG12.1, RFA. Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL. Philip, 1938.

<sup>693</sup> Haldane to "Sir", 22 September 1939, f579, b45, s401D, RG1.1, RFA.

<sup>694</sup> Philip, 1938.

<sup>695</sup> Haldane to Tisdale, 13 December 1937, b26, Haldane papers, UCL.

<sup>696</sup> Miller's diary, April 12, 1937, RG12.1, RFA. Grüneberg, 1938a.

stock, which gave him the opportunity to investigate the developmental genetics of emphysema. Grüneberg investigated this in collaboration with the tissue culturist, Honor Fell, and the pathologist, Stefan Engel.<sup>697</sup>

Grüneberg was also involved in the analysis of another pathological trait in laboratory *Rattus norvegicus* in the latter half of the decade. In December 1935 Mrs Bourne approached Haldane about an inherited cataract in her husband's rat stocks.<sup>698</sup> After Bourne had analysed the development of the cataract in the rats with his colleagues, Grüneberg helped him to genetically analyse the trait and to study the rats' eyes histologically.<sup>699</sup> The opportunist nature of such work is clearly seen from the fact that the Bourne's approached Haldane and not the other way round. This research all used rats as instances of 'organisms'.

There is one other possible case of rats being used in the department. In 1939, the Rockefeller officer, H.M. Miller, reported that work on a kinky-tailed rat was occurring in the Department of Biometry in 1939.<sup>700</sup> This work would presumably have been done by Grüneberg, who was the only mammalian geneticist at this time. However, Grüneberg's published work between 1939 and 1942 includes work on a flexed tailed mouse but not a flexed tailed rat.<sup>701</sup>

#### 4.2.2.6 Other Organisms

The other type of animal Grüneberg used for his developmental genetics work was Dachshunds. Grüneberg undertook this work from 1938 in collaboration with a Birmingham doctor, A.J. Lea. The dogs were pedigree animals, specially bred for exhibition purposes to have certain traits. These animals would have been domesticated. The work was done on two dogs kept at the DoZ/B for less

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<sup>697</sup> Fell and Grüneberg, 1939. Also see correspondence between Fell and Grüneberg, folder Fang-Firschberg, b5, Grüneberg papers. Engel and Grüneberg, 1940.

<sup>698</sup> Miller's diary, December 9-11, 1935, RG12.1, RFA.

<sup>699</sup> Bourne and Grüneberg, 1939.

<sup>700</sup> Miller's diary, November 6, 1939, RG12.1, RFA.

<sup>701</sup> Grüneberg, 1942a. Grüneberg, 1942b.



than a year. The small number of dogs arose from their size and expensiveness, which made them unsuitable for long-term research.<sup>702</sup>

Other geneticists used alternative organisms for their specialised work. Koller used the monkey, *Macacus rhesus*, in 1934/35 to investigate the cytology of spermatogenesis.<sup>703</sup> Lafon did not find any haemoglobin differences between mouse strains in 1934 and so at the start of 1935 he switched to studying locusts.<sup>704</sup> Work on these animals finished in the department when Koller and Lafon left later in 1935.

Haldane appears to have encouraged his colleagues to look for new genetic material. In 1935 Philip and Grüneberg were studying the suitability of three coleopteran species for genetic analysis,<sup>705</sup> which, as we have seen, probably resulted in Philip's use of *Dermestes vulpinus*. Spurway, similarly, began to investigate the genetics of the fin ray, *Lebistes reitculatus*, in 1937.<sup>706</sup> The investigation of such material was probably due to the usual use of animals as physical models of 'organisms' in the Department. The new material may have formed better models, or their use may have illustrated the limits of *Drosophila* and mice as models of 'organisms'.

#### 4.2.2.7 Organisms at the DoZ/B in Conclusion

The department's principle experimental organisms were wild and artificial *Drosophila*, artificial mice and humans. Domesticated organisms were barely used at the DoZ/B. This was because the study of linkage required the genetics of the organism being investigated to be manipulated. When mutations arose in domesticated organisms they were therefore bred so that their offspring were artificial. If the investigation was prolonged it was these artificial offspring, and their artificial offspring, whose genetics were investigated.

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<sup>702</sup> Grüneberg to The Secretary of Civil Service Commission, 17 May 1947, folder Larg-Lenz, b9, Grüneberg papers. Grüneberg and Lea, 1940.

<sup>703</sup> Miller's diary, October 22, 1934, RG12.1, RFA.

<sup>704</sup> Miller's diary, March 13, 1935, RG12.1, RFA.

<sup>705</sup> Work in Progress in de [sic] Department of Genetics University College, London, f578, b45, s401D, RG1.1, RFA.

<sup>706</sup> Miller's diary, April 17-22, 1937, RG12.1, RFA. Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL.

As the decade advanced the balance of organisms tipped towards wild organisms, especially *Drosophila sub-obscura*. Artificial mice and rats were retained because the opportunity to study developmental genetics arose from mutations occurring in laboratory stocks. On a practical level, such work could not easily be done with wild organisms. Humans also continued to be used as a research organism. The reason for this was that they were usually used as models for the generic group 'humans'. The work they were used for therefore could not be done with other organisms.

With the two exceptions of developmental genetics and human genetics, the research of the department changed towards the use of wild organisms. This can be related to the increasing study of the genetics of evolution in the department. This favoured the use of wild organisms but it did not preclude the use of artificial organisms. Christie studied homology with artificial *Drosophila melanogaster* and Minns used them to study mating preferences. The switch to wild animals also occurred as Haldane became interested in the effects of domestication. This made him concerned that artificial/domesticated animals were not good physical models for 'organisms'.

The switch to wild animals may have been expected to decrease the use of research animals as model organisms because it involved the recognition that not all organisms are the same. However, this was not seen at the DoZ/B. This is probably because the work the group conducted concerned the genetic analysis of wild populations. Genetic analysis can only be done by using a theory that relates phenotype to genes, ignoring the influence of other factors. Since all organisms have genes, a focus which ignores all other factors encourages all organisms to be viewed as essentially the same. The department's geneticists were cautious about using organisms as models of 'organisms'. Philip's work with *Dermestes* was portrayed as a check on the work with *Drosophila*.

#### **4.2.3 Organisms used at the IAG**

In this section I investigate the organisms used at the IAG during the 1930s. This shows they were almost all domesticated. The range of domesticated organisms was much greater than at the DoZ/B. Laboratory animals, agricultural animals, pedigree animals and even horticultural plants were studied. The focus on *Drosophila* and mice at the DoZ/B had no counterpart at the IAG. A wide range of organisms were used reasonably extensively for research. Geneticists tended to remain low down the is-a hierarchy, except when using laboratory animals or miscellaneous animals. These latter two groups were used for more formal genetic research (see Chapter Five, section 5.2.2) at the IAG. The purpose of such research was to gain information that could be applied to organisms that were different in type. This required the geneticists to move up the is-a hierarchy. However, they tended to make such generalisations from information gained from more than one organism. As such the research organisms did not act as 'models' but 'instances' of the type group 'organisms'. This changed following the arrival of H.J. Muller. Formal genetics then became more important and the influence of the more applied work weakened.

#### 4.2.3.1 Farm Animals

As may be expected from the location's agricultural heritage, many of the animals used at the Institute were farm animals. In this section I show that the most extensively researched of these were the most economically valuable: pigs, sheep, poultry and cattle. These animals were used both as the physical models of groups low down the is-a hierarchy and to gain information about 'organisms'.

Cattle were used for research at the Institute throughout the 1930s. Between 1927 and 1933 research was done under the direction of A.D. Buchanan Smith into the degree of inbreeding that existed in the Shorthorn breed of cattle.<sup>707</sup> Buchanan Smith also directed work into the inheritance of milk yield from at least 1932.<sup>708</sup> It is likely that this work continued until at least 1939, as the Scottish Milk Marketing Board gave an annual grant for work on dairy cattle from 1935 until

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<sup>707</sup> Buchanan Smith to Wright, 15 March 1933, folder Buchanan Smith, A[lick] D, Wright papers. Wright to Buchanan Smith, April 13, 1933, folder Buchanan Smith, A[lick] D, Wright papers.

<sup>708</sup> Goodale to Buchanan Smith, June 30, 1932, folder Buchanan Smith, A.D., Goodale papers.

then.<sup>709</sup> Both of these studies used cattle as the physical models of 'cattle'. The former studied the extent of a genetic phenomenon in cattle; the latter studied how milk yield could be increased in cows in particular.

In 1927 the Institute acquired a pig testing station. The station investigated the registry of bacon pigs<sup>710</sup> until at least 1931.<sup>711</sup> The research focused on registry as it affected pigs and thus pigs were used as physical models of the type group 'pigs'. This is true of the other researches conducted with pigs at the Institute. Research into the genetics of pigs was carried out by Buchanan Smith from 1932.<sup>712</sup> In 1933 the research investigated how weight gain in pigs related to the amount of food they were fed.<sup>713</sup> Again the results applied specifically to pigs. From 1938 the Institute worked to create an inbred strain of pigs, with disappointing results.<sup>714</sup> Genetic results were thus applied to pigs, making them physical models of 'pigs'. It may have been the inability of the IAG to create inbred pigs that led Koller to research the cytology of pigs in 1938/39. By doing so he explained why genetical studies with pigs and breeding a number of traits into pigs were generally difficult.<sup>715</sup> Again, the results applied specifically to pigs.

Sheep were another farm animal extensively studied at the Institute during the 1930s. In 1928 the Institute received a five year grant from the Empire Marketing Board for research into sheep. Work on the genetics, sex physiology and biology of fleeces was conducted under Miller.<sup>716</sup> This work all used sheep as physical models of 'sheep' since findings about the fleece of sheep were only relevant to sheep. The funding for this research from the Empire Marketing Board ended in March 1933, but the research continued with support from the ARC until

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<sup>709</sup> F1, folder Minutes, IAGA. F2, folder Minutes, IAGA. M23, folder Minutes, IAGA.

<sup>710</sup> A7, folder Memos, financial reports, IAGA.

<sup>711</sup> M9, folder Minutes, IAGA.

<sup>712</sup> Memo 4, folder Memos, financial reports, IAGA.

<sup>713</sup> Miller's diary, April 28, 1933, RG 12.1, RFA. Buchanan Smith soundclip, <http://epona.lib.ed.ac.uk:1821/media/sound.html>, accessed 6 January 2004.

<sup>714</sup> Annual Report, 1938-1939, folder IAG Annual Reports, IAGA.

<sup>715</sup> Annual Report, 1938-1939, folder IAG Annual Reports, IAGA. Koller to Demerec, 8 March 1939, folder Koller, Peo C #1, Demerec papers.

<sup>716</sup> A8, folder Memos, financial reports, IAGA. Memo 4, folder Memos, financial reports, IAGA. Miller's diary, April 28, 1933, RG12.1, RFA. Kemp to Tisdale, August 10, 1934, f44, b4, s405D, RG1.1, RFA.

1935.<sup>717</sup> At that time Miller left the department and work on sheep was discontinued.<sup>718</sup> In 1939 however, some work was done on sheep at the department, comparing the cytology of different breeds.<sup>719</sup> This work used different breeds as instances of sheep in general. Thus sheep were used as physical models of their breed, and a generalisation about sheep was made from the breeds.

The one exception to using farm animals as physical models of groups low down the is-a hierarchy were fowl. These animals were used to model the type group 'fowl', but they were also used as instances of 'organisms'. During the 1930s fowl were used for two distinct forms of research. The first was sex physiology. This work was conducted under the direction of Alan Greenwood throughout the 1930s.<sup>720</sup> Such research included studies of sexual dimorphism of the plumage of fowl and how testis affected this. This research used fowl to model the group 'fowl'. The other major use of fowl at the Institute was for transmission genetics and cytological work, which was carried out under Crew's direction throughout the decade.<sup>721</sup> This work also used fowl to model the group 'fowl'. For example, Crew and Munro studied the genetics of asymmetry in fowl. However, fowl were also used as instances of 'organisms' in the work. For example, Crew studied the sex ratio of fowl and used this to talk about sex-linked lethal genes. The latter was of relevance to all organisms, but Crew did not generalise from the fowl to all organisms. He thus used fowl as instances of 'organisms' rather than as models of 'organisms'.

While fowl and cattle, and to a lesser extent pigs and sheep, were the main farm animals researched at the IAG, a number of other farm animals were also used. Horses were kept at the Institute during the decade. Work was done by Miller on

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<sup>717</sup> M17, folder Minutes, IAGA.

<sup>718</sup> Anonymous to Sir Thomas, 10 October 1935, folder IAG Annual Reports, IAGA.

<sup>719</sup> Annual Report, 1939-1940, folder IAG Annual Reports, IAGA.

<sup>720</sup> A8, folder Memos, financial reports, IAGA. Greenwood and Blyth, 1932. Greenwood and Blyth, 1938a. Greenwood and Blyth, 1938b.

<sup>721</sup> A8, folder Memos, financial reports, IAGA. Crew to Dunn, April 1, 1933, folder Crew, F.A.E., Dunn papers. Weaver's diary, May 11, 1935, RG12.1, RFA. Crew, 1938. Crew and Munro, 1939.

diagnosing pregnancy in horses in 1932<sup>722</sup> and Buchanan Smith investigated their genetics generally at the start of the 1930s.<sup>723</sup> Ducks, turkeys and geese were all used for general genetics work.<sup>724</sup> Goats were also used to investigate the inheritance of their milk yield and constitution.<sup>725</sup> This work all used the organisms as physical models of groups low down the is-a hierarchy.

In general, farm animals were investigated because the purpose of the IAG was to provide agriculturalists with information about animal breeding.<sup>726</sup> This required information to be gained about the breeding of farm animals in particular. Farm animals were therefore used, at the Institute, as physical models of groups of farm animals. The ones most investigated were the ones most economically valuable to agriculturalists. This was probably because the ARC was more likely to provide funding for such research. The one exception is fowl. These were researched to gain information both about the group 'fowl' and to gain information about the type group 'organisms'. Fowl were traditionally used for genetics research and thus they were used by the department's pure geneticists, who used them as instances of 'organisms', as well as by the sex endocrinologists who studied them as physical models of 'fowl'.

#### 4.2.3.2 Pedigree Animals

Pedigree animals were also used at the IAG for genetics research. Such animals were bred by amateurs to have traits that conformed to a pre-determined standard. The animals were then exhibited at local and national shows. Pedigree animals were often taken up for study by geneticists because they tended to have reasonably uniform genetics and pedigree breeders often spotted new and interesting mutations. In this section I show that a variety of pedigree animals

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<sup>722</sup> Memo 4, folder Memos, financial reports, IAGA. Anonymous to Sir Thomas, 10 October 1935, folder IAG Annual Reports, IAGA.

<sup>723</sup> Miller's diary, April 28, 1933, RG12.1, RFA.

<sup>724</sup> Memo 4, folder Memos, financial reports, IAGA. The work on ducks also included genetical and cytological work on a hybrid of the muscovy duck and the white crested spadebill. (Crew and Koller, 1936).

<sup>725</sup> A7, folder Memos, financial reports, IAGA. Memorandum – Application for a Special Grant for Research on Pig and Goat-Breeding, folder Memos, financial reports, IAGA.

<sup>726</sup> A7, folder Memos, financial reports, IAGA.

were studied, but only rabbits were studied to any great extent. In all cases, they were used as physical models of groups low down the is-a hierarchy.

The most extensively studied of the pedigree animals were rabbits. Like fowl, rabbits had long been used for genetics research. However, rabbits were used at the IAG because they were economically valuable.<sup>727</sup> Throughout the decade, James Pickard attempted to improve the wool obtained from Angora rabbits and produce different varieties of pelt.<sup>728</sup> He did so by researching the inheritance of coat colour in rabbits and their genetics in general.<sup>729</sup> Token rabbits were therefore used as physical models of type 'rabbits'.

Though no other pedigree animal was extensively researched at the Institute, Crew was especially keen on using such animals. The head of the NS, Warren Weaver, recorded in his 1935 diary:

“He [Crew] talks somewhat fantastically of the ‘importance’ of the parakeet and canary industries, saying that fanciers are interested in genetics, while the cow, horse, sheep, and swine people are not.”<sup>730</sup>

Crew was using parakeets and canaries for transmission genetics studies when Weaver visited the Institute.<sup>731</sup> According to one of Weaver's officers, H.M. Miller, Crew received budgerigars and canaries from fanciers for his genetics work.<sup>732</sup> Crew and Rowena Lamy also published a book on the genetics of the budgerigar in 1935.<sup>733</sup> Crew and Lamy therefore used pedigree animals because they could gain them easily and because there was a constituency interested in their results. Due to the latter the animals were used as physical models of groups of pedigree animals in the research.

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<sup>727</sup> A7, folder Memos, financial reports, IAGA.

<sup>728</sup> Memo 4, folder Memos, financial reports, IAGA.

<sup>729</sup> A8, folder Memos, financial reports, IAGA.

<sup>730</sup> Weaver's diary, May 11, 1935, RG12.1, RFA.

<sup>731</sup> Weaver's diary, May 11, 1935, RG12.1, RFA.

<sup>732</sup> Miller's diary, December 6 and 7, 1935, RG12.1, RFA.

<sup>733</sup> Crew and Lamy, 1935b.

Cats and dogs were both kept at the Institute during the 1930s.<sup>734</sup> In 1939 Koller began to study the cytology of cats in collaboration with Darlington of the JI.<sup>735</sup> Cytological studies were also carried out on different breeds of dogs in 1939/40.<sup>736</sup> Dogs had previously been used by Wiesner in the department for sex physiology work.<sup>737</sup> Koller used cats and dogs because he was interested in the cytology of mammals in general, as discussed in section 4.2.3.4 below. The cats and dogs were not of interest themselves, but they also did not form models of mammalian cytology. Their cytology was treated as an instance of mammalian cytology, such that the differences and similarities could be identified. Thus, as for farm animals, pedigree animals were generally used as physical models of groups low down the is-a hierarchy, but they were also used as instances of higher groups; in this case mammals.

#### 4.2.3.3 Laboratory Animals

As geneticists took up pedigree animals for genetic research, they tried to standardise them further and convert them into laboratory animals, over which they alone had control. Karen Rader has described how C.C. Little took mice from breeders and made them part of the scientific domain by connecting them to genetics problems and giving the strains names based on their genetics, rather than their appearance.<sup>738</sup> Robert Kohler has similarly discussed how wild *Drosophila* became domesticated by scientists.<sup>739</sup> In this section I show that the IAG, like the DoZ/B, used a variety of laboratory animals for their research. Most of these were artificial, some were domesticated, and a few were wild. These animals were mainly used as instances of 'organisms'. They were also used as physical models of groups low down the is-a hierarchy and, from the time Muller joined the department at the end of 1937, *Drosophila* were also used as models of 'organisms'.

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<sup>734</sup> Weaver's diary, May 11, 1935, RG12.1, RFA.

<sup>735</sup> Koller to Dobzhansky, 3 July 1939, folder Koller, Pius Charles, Dobzhansky papers.

<sup>736</sup> Annual Report, 1939-1940, folder IAG Annual Reports, IAGA.

<sup>737</sup> Memo 4, folder Memos, financial reports, IAGA.

<sup>738</sup> Rader, 1999.

<sup>739</sup> Kohler, 1994, chapter two.



Rats were extensively used for research at the IAG during the 1930s. In 1929/30 there were approximately 800 rats at the IAG, which included Wistar rats imported from Philadelphia.<sup>740</sup> A year later the number of rats in the department had risen into the thousands.<sup>741</sup> During the year the rats were inbred brother-to-sister.<sup>742</sup> The rats used at the Institute were therefore artificial.

In the first half of the decade these rats were used extensively for genetics work, sex physiology, research into senility,<sup>743</sup> and to repeat McDougall's Lamarckian experiments.<sup>744</sup> This research appears to have used rats as instances of 'organisms'. The work of Hain and Robson, for example, compared the physiology of rats and mice. Generalisations about 'organisms' were therefore not made on the basis of one organism.<sup>745</sup> Crew's work disproved McDougall's finding that learning could be inherited in rats.<sup>746</sup> The research was of relevance to organisms in general. However, Crew did not use the rats as models of 'organisms', since he did not generalise from his findings. He disproved an anomaly to an existing generalisation. In 1933, Bryden compared the cytology of mice and rats.<sup>747</sup> This work again used rats to provide an instance of a process in 'organisms'.

Research with rats declined during the decade. This was due to the loss of the sex physiology section between 1932 and 1935 from a lack of financial support, and the completion of Crew's repetition of McDougall's work in 1935/1936. However, some rat-based work was still being done in 1938.<sup>748</sup>

Mice were also used extensively at the IAG throughout the 1930s. They were sometimes used as physical models of 'mice' in genetic, physiology or cytology investigations. More often they were used as instances of 'organisms', as

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<sup>740</sup> Annual Report, 1929-1930, folder IAG Annual Reports, IAGA. Interview with Crew, CD 7, IAGA.

<sup>741</sup> M10, folder Minutes, IAGA.

<sup>742</sup> Annual Report, 1929-1930, folder IAG Annual Reports, IAGA.

<sup>743</sup> Memo 4, folder Memos, financial reports, IAGA. A8, folder Memos, financial reports, IAGA.

<sup>744</sup> Crew to Dunn, April 1, 1933, folder Crew, F.A.E., Dunn papers. Annual Report, 1935-1936, folder IAG Annual Reports, IAGA.

<sup>745</sup> Hain and Robson, 1936.

<sup>746</sup> Interview with Crew, CD 7, IAGA.

<sup>747</sup> Bryden, 1933.

<sup>748</sup> Annual Report, 1937-1938, folder IAG Annual Reports, IAGA.

discussed in section 4.4. The mice were usually artificial, but were occasionally domesticated. For example, Crew and Auerbach's work on the character 'Rex' made use of domesticated Rex mice, given to them by a mouse breeder. They crossed a male Rex mouse with female mice from an inbred line containing Caracul. They then crossed the offspring with an inbred line that contained neither allele. These latter two mice were both artificial, as were the resultant offspring.<sup>749</sup> In 1939/1940, wild mice were also used at the IAG. Koller compared the chromosomes of two species of field mouse, *A. sylvaticus* and *A. hebridensis*.<sup>750</sup>

*Drosophila* were also extensively researched at the IAG. Three species of *Drosophila* were used throughout the decade. The first is *Drosophila melanogaster*. Koller brought artificial, inbred *D. melanogaster* back to Edinburgh following a visit to Curt Stern in Berlin in 1929.<sup>751</sup> Inbred, and thus artificial, *Drosophila pseudo-obscura* were also available at the Institute from 1930<sup>752</sup> and *Drosophila obscura* from at least 1932.<sup>753</sup> These artificial organisms were used for a variety of transmission genetics research<sup>754</sup> and developmental genetics.<sup>755</sup> These studies tended to use *Drosophila* as physical models of 'Drosophila'.<sup>756</sup>

Following the arrival of H.J. Muller in 1937 work with *Drosophila* expanded to include the investigation of mutagenesis.<sup>757</sup> This work is the first example of animals being consistently used as models of 'organisms' at the IAG. The work tried to discover how radiation causes gross structural re-arrangements in chromosomes in general, rather than the chromosomes of *Drosophila* in particular.<sup>758</sup> The influence of Muller seems to have led Koller to use *Drosophila*

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<sup>749</sup> Crew and Auerbach, 1939.

<sup>750</sup> Annual Report, 1939-1940, folder IAG Annual Reports, IAGA.

<sup>751</sup> Koller to Stern, 25 September 1929, folder Koller, Peo Charles, Stern papers. Koller to Stern, 23 October 1929, folder Koller, Peo Charles, Stern papers.

<sup>752</sup> Koller, 1936b, 80.

<sup>753</sup> Koller, 1932b.

<sup>754</sup> A8, folder Memos, financial reports, IAGA.

<sup>755</sup> Miller's diary, December 6 and 7, 1935, RG 12.1, RFA.

<sup>756</sup> See, for example, Crew and Lamy, 1931/1932.

<sup>757</sup> Crew to "Sir", 17 February 1938, f44, b4, s405D, RG 1.1, RFA. Memorandum on the Needs of the *Drosophila* Work at the IAG, University of Edinburgh, f44, b4, s405D, RG1.1, RFA.

<sup>758</sup> See Chapter Five for details of this work. Muller, 1940.

*miranda* as a model of ‘organisms’ following his return from his RF fellowship. Koller collected the organisms during field trips he took while on his fellowship.<sup>759</sup> They were therefore wild animals. The Annual Report for 1938/39 stated that his findings about the cytology of *D. miranda* hybrids:

“may be considered as a further observation upon the mechanism which leads to species differentiation isolation through sterility.”<sup>760</sup>

Guinea pigs also appear to have been used in the department for research purposes, but no information is available on what this research was, and it seems unlikely that they were extensively utilised.<sup>761</sup>

The laboratory animals used at the IAG tended to be artificial. However, some domesticated laboratory animals were used because new mutations were often found in them. Wild laboratory animals were also used towards the end of the decade. The latter were usually used to compare the cytology of two species or races. As seen at the DoZ/B, wild animals were usually favoured for research on evolution, such as this. Laboratory animals were not generally used by geneticists because they were interested in the genetics of these organisms in particular. They were used because they were more likely to reveal principles of genetics. Crew faced opposition to the use of laboratory animals because the IAG was a breeding location.<sup>762</sup> By justifying the use of laboratory animals as more likely to reveal genetics principles, Crew was arguing that academic activities were an integral part of a breeding genetics research programme.

The institutional culture against using organisms as models of the type ‘organisms’ was clearly seen in the use of laboratory animals. Information was gained about the type group ‘organisms’ by using laboratory animals as instances of ‘organisms’. Only after Muller arrived, at the end of 1937, were laboratory animals, especially *Drosophila*, used as models of ‘organisms’. Some research was also done at the IAG to find out more about laboratory animals. The more

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<sup>759</sup> Koller to Dobzhansky, 23 January 1939, folder Koller, Pius Charles, Dobzhansky papers.

<sup>760</sup> Annual Report, 1938-1939, folder IAG Annual Reports, IAGA.

<sup>761</sup> Report and List of Publications for the year 1936-1937, folder IAG Annual Reports, IAGA.

<sup>762</sup> Report and List of Publications for the year 1936-1937, folder IAG Annual Reports, IAGA.

that was known about them the easier laboratory animals were to use for other investigations. Thus, in some cases they were used as physical models of groups of laboratory animals.

#### 4.2.3.4 Miscellaneous Organisms

A very wide range of organisms other than those mentioned were used for research at the IAG. None were used extensively. Most were domesticated or wild mammals. This enabled them to be used as a physical model for mammals, of which farm mammals (cattle, pigs, sheep, horses) were a sub-set of interest to the Institute. Research was also done on organisms that were used as physical models for groups lower down the is-a hierarchy, for example humans as models of 'humans'.

Two types of research were undertaken with mammals. The first was comparative cytological research. During the mid-1930s Koller compared chiasmata in various wild animals, including the marsupial cat and Tasmanian devil.<sup>763</sup> At a similar time, he also compared the sex chromosomes of various domesticated mammals, including humans, marsupials<sup>764</sup> and the golden hamster.<sup>765</sup> The mammals studied were not of interest themselves but acted as examples of mammalian cytogenetics. They helped to define the range of cytogenetical processes and fundamental similarities in mammals. Such findings could then be applied to farm mammals. As such the organisms did not act as models of 'mammals', but as a set of examples, to which analogies could be made.

The second type of work with mammals investigated their sexual physiology. Monkeys were used by Wiesner for sex physiology work at the start of the decade.<sup>766</sup> Koller studied the cytology of their reproductive organs while at the DoZ in 1934/35. This work formed part of the programme of studies he began at the IAG. This programme included research into the behaviour of chromosomes

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<sup>763</sup> Koller, 1936a.

<sup>764</sup> Koller, 1936c.

<sup>765</sup> Koller, 1938a.

<sup>766</sup> Memo 4, folder Memos, financial reports, IAGA.

in the reproductive organs of male grey squirrels<sup>767</sup> and the behaviour of sex chromosomes in ferrets and moles during anoestrus.<sup>768</sup> All these mammals were wild. Mammals were studied for such investigations because of their method of reproduction. This they shared with humans and many of the economically valuable species studied in the department.

Human genetics was researched by J.A. Fraser Roberts between 1931 and 1933, before he left the Institute.<sup>769</sup> In 1935/36 Koller began to study partial sex linkage in man cytologically.<sup>770</sup> In 1937/38 he completed this work, which involved a detailed study of the sex chromosomes. The work was presumably conducted with humans being used as physical models of 'humans'.

Koller's work on the cytology of the reproductive cycle was the basis of H.D. Slack's PhD study on the cytology of sperm formation. For this, he used twenty species of the water boatman family.<sup>771</sup> Following this study, sperm formation was also investigated in the Indian locust.<sup>772</sup> Both these studies used wild animals and because they formed part of a comparative programme, they used the animals as instances of spermatogenesis.

Plants were also researched to a limited extent at the IAG. In 1935 Koller published an article on the cytology of hawksbeard and golden hawksbeard. It is possible that this work was done while he was still in London. However, since there was plenty of land at the Institute, and these plants are wild, it is perfectly possible that he conducted the work at the Institute.<sup>773</sup> In 1936/37 Koller investigated the cytology of sterile peas at the IAG.<sup>774</sup> Sterility was obviously of interest to a breeding research centre. Peas were used because sterility arose in them and Koller managed to obtain some sterile plants. Their genetics were also

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<sup>767</sup> Koller, 1936e.

<sup>768</sup> Annual Report, 1936-1937, folder IAG Annual Reports, IAGA. Koller, 1936d.

<sup>769</sup> Memo 4, folder Memos, financial reports, IAGA. A8, folder Memos, financial reports, IAGA. Polani, 1992, 309.

<sup>770</sup> Annual Report, 1935-1936, folder IAG Annual Reports, IAGA.

<sup>771</sup> Annual Report, 1937-1938, folder IAG Annual Reports, IAGA.

<sup>772</sup> Annual Report, 1939-1940, folder IAG Annual Reports, IAGA.

<sup>773</sup> Koller, 1935a.

<sup>774</sup> Koller to Darlington, 1 November 1936, folder J.125, box c.110, Darlington papers. Annual Report, 1937-1938, folder IAG Annual Reports, IAGA. Koller, 1938b.

well established, since the sterile plants arose at the JI.<sup>775</sup> These plants were therefore domesticated.

The miscellaneous organisms used at the IAG were mainly used to investigate the similarities and differences in the cytogenetics of animals. They were thus used as instances and not usually because there were of interest themselves. The mammals used formed physical models of mammals in general because a sub-set of this group, farm mammals, was of interest to the Institute. The miscellaneous organisms used were both wild and domesticated.

#### **4.2.3.5 Organisms at the IAG in Conclusion**

The organisms used at the IAG fall into three main categories: farm animals, pedigree animals and laboratory animals. The former two were generally studied as physical models of groups low down the is-a hierarchy. The purpose of the Institute was to provide information about breeding animals to agriculturalists,<sup>776</sup> hence the study of farm animals. Fanciers provided an audience for the Institute's work and so Crew researched pedigree animals for information about their particular breeding too. However, pedigree animals were not always researched because they were of interest, and so research use cannot be predicted from the type of organism. For example, cats and dogs were studied because they were mammals, and thus physical models of this group. Despite being pedigree animals they were studied as instances of 'mammals' rather than as physical models of 'cats' and 'dogs'.

Laboratory animals were also used as both instances of 'organisms' and physical models of a group of laboratory animal. The use of laboratory animals at a breeding location was unexpected. Crew justified it by arguing that academic activities were an important part of a breeding research programme. The use of laboratory animals as physical models of groups of laboratory animals was also unexpected, as these groups are not usually considered to be of interest. However, information about the genetics of laboratory organisms in particular

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<sup>775</sup> Annual Report, 1937-1938, folder IAG Annual Reports, IAGA.

<sup>776</sup> A7, folder Memos, financial reports, IAGA.

was sought by other professional geneticists. Thus, there was an audience for such work. It was more usual to use laboratory animals to provide information about 'organisms'. At the IAG this was usually done by using the animals as instances of genetics in organisms in general, rather than as models of 'organisms'. At the end of 1937 Muller arrived at the Institute and took control of the *Drosophila* group.<sup>777</sup> *Drosophila* were used as models of 'organisms' from then on. Until the arrival of Muller there was therefore an institutional culture that resisted the use of animals as models of 'organisms'.

Another distinctive feature of the IAG was the predominant use of domesticated animals for research. Artificial, wild and miscellaneous animals were also used throughout the decade.

#### **4.2.4 Types and Uses of Organisms in Conclusion**

There were two major differences between the organisms used at the DoZ/B and the IAG: the types of organisms they used and how they used them. Both locations used a mixture of artificial, domesticated and wild organisms. However, the DoZ/B increasingly used wild organisms during the decade and rarely used domesticated organisms at any time during the decade. The IAG, in contrast, mainly used domesticated organisms. This difference arose from the differential functions of the two locations. The purpose of the IAG was to provide information about animal breeding to agriculturalists, hence the need to research farm animals, which were domesticated. The purpose of the DoZ/B was to increase understanding about animals. As Haldane started to perceive laboratory animals as problematic physical models for 'organisms' the geneticists moved to using wild animals.

The other major difference between the locations was the way they used research organisms. At the DoZ/B animals were used either as models of 'organisms' or instances of 'organisms'. At the IAG many of the organisms studied were used as physical models of groups at a low level of the is-a hierarchy. This was true even

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<sup>777</sup> Crew to Sir, 17 February 1938, f44, b4, s405D, RG1.1, RFA.

of laboratory animals. Where organisms were used to provide information about 'organisms' it was usual to use individual organisms or species as instances of 'organisms' rather than models of 'organisms'. The latter only became an acceptable practice at the IAG following the employment of Muller. This difference can also be traced to the difference in the locations' purpose. The purpose of the DoZ/B was to increase understanding about animals in general, not any particular animals. It was therefore necessary for them try to gain information about 'organisms'. At the IAG the purpose of the location was to provide information about animal breeding to agriculturalists. This necessarily meant they used farm animals as physical models of farm animals. As geneticists saw the difficulties of applying current genetic theory to such animals, it made them cautious about using any organism as a model for 'organisms'. Hence the favoured use of organisms as instances of 'organisms' rather than models of 'organisms'.

### **4.3 Research Organisms at Other Genetic Locations in Britain**

In this section I investigate the types of organisms used for research at other locations for genetics in 1930s Britain. This demonstrates that the differences seen between the IAG and the DoZ/B were typical of differences between their settings.

#### **4.3.1 Research Organisms in the Academic Setting**

In this section I demonstrate that it was typical of zoology departments in the British academic setting to focus research on wild and artificial animals. It was also typical to use organisms to make conclusions about generic 'organisms' through either instances or models. Botany departments in the British academic setting tended to investigate domesticated and wild plants. It is unclear whether the organisms they studied were used as physical models of 'organisms' or groups lower down the is-a hierarchy.



Most of the organisms used in British zoology departments were wild animals. As well as their use at the DoZ/B, when Gordon moved to Aberdeen from the DoZ/B he continued his work with wild *Drosophila* and began to work with wild rabbits<sup>778</sup> and a local isopod.<sup>779</sup> There were some exceptions to this predominance of wild organisms. For example, at the Department of Zoology, in the University of Liverpool, Ruth Bamber<sup>780</sup> and E.C. Herdman studied the genetics of cats, which were domestic animals. With the possible exception of the cats, all the animals were used to gain information about 'organisms'.

While none of the zoology departments studied domesticated organisms of commercial value, botany and genetics departments did. The major research organisms at the Department of Genetics at Cambridge were poultry. Poultry had well established genetics, making them very useful research organisms. Punnett also studied sweet peas to a reasonable extent. Sweet peas also had a long history in genetics research. He and Bateson had studied their genetics in the first decade of the twentieth century.<sup>781</sup> Punnett researched rabbits, cattle and cuckoos to a lesser extent. Punnett's choice of major research organisms appears to have been made long before the 1930s, when the number of locations in the academic setting greatly expanded. His choice was therefore slightly atypical for the time, in as much that they were generally domesticated and commercially valuable. Though the commercial value of Punnett's organisms made them of interest themselves, he used them to make findings about genetics in general.<sup>782</sup>

Botany departments would have found it difficult not to research organisms of commercial value. They appear to have taken advantage of their connection to horticulture to gain extra funding as discussed in Chapter Three (section 3.4.1). Thus, a mixture of flowers and vegetables were used for genetic analysis at the Department of Botany at Manchester University. In 1936 a Rockefeller officer, H.M. Miller, recorded that the Sansomes were studying genetics with dahlias,

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<sup>778</sup> Tisdale's diary, June 27-28, 1937, RG12.1, RFA. Grant in aid 37187, f39, b3, s405D, RG1.1, RFA.

<sup>779</sup> Miller's diary, November 18 and 19, 1938, RG12.1, RFA.

<sup>780</sup> Bamber and Herdman, 1932. Bamber, 1933.

<sup>781</sup> Crew, 1967, 324-326.

<sup>782</sup> Crew, 1967, 318.

roses, tomatoes and peas.<sup>783</sup> These all had obvious connections to gardening and were all domesticated organisms. They were of interest themselves but this does not mean they were not used to make generalisations about ‘organisms’.<sup>784</sup>

The largest group of geneticists in a botanical department was, however, that of Gates at King’s College, London. The group primarily worked with *Oenothera* (evening primrose),<sup>785</sup> and were commonly known as the *Oenothera* school.<sup>786</sup> Gates first used *Oenothera* when working at Woods Hole. The head of botany at Woods Hole, B.M. Davis, had obtained some seeds from de Vries, and Gates took part in the study.<sup>787</sup> Gates began working with *Oenothera* because it was available at Woods Hole. This highlights the importance of access to organism choice, as pointed out by Clarke.<sup>788</sup> Davis and Gates were interested in *Oenothera*, however, because it suggested that evolution could occur by mutation. *Oenothera* remained an important organism for Gates because it was a highly productive research organism, which gave rise to results that questioned some of the new theories on evolution and heredity.<sup>789</sup> *Oenothera* was therefore not used as a model of ‘organisms’. However, it was used because its results were of interest beyond *Oenothera*, itself. As such, it was used as an instance of ‘organisms’.

It was therefore typical for British zoology departments to research wild animals to a greater extent than artificial or domesticated animals. They also tended to use them to make conclusions about ‘organisms’. Botany departments, and the genetics department at Cambridge, tended to work on commercially important, domesticated organisms. However, the example of King’s College, London shows that they were not necessarily used primarily because they were commercially valuable. Gates and Punnett both used such organisms to gain information about the type group ‘organisms’. It is therefore likely that the

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<sup>783</sup> Miller’s diary, January 31, 1936, RG12.1, RFA. See also, Miller’s diary, October 21, 1937, RG12.1, RFA.

<sup>784</sup> See for example, Sansome (F.W.), 1937/1938 and Sansome (E.R.), 1938.

<sup>785</sup> See for example, Catcheside, 1933.

<sup>786</sup> Darlington, 1998, 70.

<sup>787</sup> Fraser Roberts, 1964, 85.

<sup>788</sup> Clarke, (Adele), 1987, 326, 340.

<sup>789</sup> Fraser Roberts, 1964, 86-89.

organisms were used to make conclusions at a range of levels along the is-a hierarchy.

#### 4.3.2 Research Organisms in the Breeding Setting

In this section I show that most of the organisms used in the breeding setting were domesticated and commercially valuable. The organisms were used as physical models of groups low down the is-a hierarchy, rather than 'organisms'.

Horticultural organisms and agricultural organisms were used in the setting. Both were domesticated. Horticultural organisms dominated at the JI, as may be expected for a horticultural location. Throughout the decade research was done on the genetics of domesticated flowers, such as *Primula*,<sup>790</sup> *Dahlia*,<sup>791</sup> *Tradescantia*,<sup>792</sup> *Lathyrus odoratus*,<sup>793</sup> *Antirrhinum majus*,<sup>794</sup> *Nicotiana langsdorffii* and *sanderiae*,<sup>795</sup> *Cheiranthus cheiri*,<sup>796</sup> *Tropaeolum majus*,<sup>797</sup> *Tulipa*,<sup>798</sup> *Campanule persicifolia*<sup>799</sup> and *Streptocarpus*.<sup>800</sup> Also studied were the genetics of fruit: raspberry plants,<sup>801</sup> apples,<sup>802</sup> pears<sup>803</sup> and tomatoes<sup>804</sup>; vegetables such as peas<sup>805</sup>; and herbs such as *Avena*.<sup>806</sup> The genetics of trees were also studied, such as the red horse chestnut.<sup>807</sup> Some animals with horticultural links were studied such as grasshoppers<sup>808</sup> and pond snails.<sup>809</sup> The JI studied agricultural plants too, such as oats<sup>810</sup> and maize<sup>811</sup> and pathogens of

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<sup>790</sup> de Winton and Haldane, 1933. de Winton and Haldane, 1935. Haldane, 1936a.

<sup>791</sup> Lawrence, 1931. Lawrence and Scott-Moncrieff, 1935.

<sup>792</sup> Koller, 1932a.

<sup>793</sup> Stone, 1932. Beale, Robinson, Robinson and Scott-Moncrieff, 1938/1939.

<sup>794</sup> Gairdner and Haldane, 1933.

<sup>795</sup> Brieger, 1935.

<sup>796</sup> Gairdner, 1936.

<sup>797</sup> Moffett, 1936. Sutton, 1939.

<sup>798</sup> Upcott and La Cour, 1936. Upcott, 1937. Upcott, 1938/1939. Upcott and Philp, 1939.

<sup>799</sup> Darlington and Gairdner, 1937/1938.

<sup>800</sup> Lawrence, Scott-Moncrieff and Sturges, 1939.

<sup>801</sup> Crane and Lawrence, 1931. Lewis, 1939.

<sup>802</sup> Crane and Lawrence, 1933/1934. Lewis and Crane, 1938/1939.

<sup>803</sup> Crane and Thomas, 1938/1939.

<sup>804</sup> Fabergé, 1936.

<sup>805</sup> Pellew and Sansome (E.R.), 1931/1932.

<sup>806</sup> Philp, 1933.

<sup>807</sup> Upcott, 1936.

<sup>808</sup> Sansome (F.W.) and La Cour, 1935.

<sup>809</sup> Diver and Andersson-Kottö, 1937/1938.

<sup>810</sup> Philp, 1935.

such plants, such as *Diaporthe pernicioso*.<sup>812</sup> These were presumably studied because they had commercial value and were thus used as physical models of groups low down the is-a hierarchy. The plants were all domesticated, the animals and pathogens wild.

The JI also studied the genetics of wild flowers, such as *Silene otites*,<sup>813</sup> *Papaver*<sup>814</sup> and *Lythrum salicaria*,<sup>815</sup> and wild plants such as ferns<sup>816</sup> and herbage grasses.<sup>817</sup> Some of the interest in them regarded how their cytology compared to garden plants. In this case, the organisms were used as instances of wild plants. The rest of the work may have originated from Haldane's interest in domestication, since he also directed genetics work at the JI during the early 1930s. Humans<sup>818</sup> and artificial *Drosophila melanogaster*<sup>819</sup> were also studied at the JI. The latter was used as a model of 'organisms'; the former was used as a physical model of 'humans', due to Haldane's interest in human genetics in particular.

The rest of the breeding locations specialised to a far greater extent than the IAG and the JI. Most of the genetics research at the Plant Breeding Institute was done on wheat.<sup>820</sup> However, oats and soya-bean were also used.<sup>821</sup> The genetics of radishes, turnips, cabbages, wheat and the domesticated flower, *Paeonia*, were also studied at the Cambridge School of Agriculture,<sup>822</sup> of which the Plant Breeding Institute was part.

At the Scottish Plant Breeding Station, studies were done on the genetics of potatoes,<sup>823</sup> oats<sup>824</sup> and *Brassica napus*, which includes crops such as oil seed

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<sup>811</sup> Brieger, 1937. Brieger, Tidbury and Tseng, 1938.

<sup>812</sup> Cayley, 1931.

<sup>813</sup> Newton, 1931.

<sup>814</sup> Philp, 1933/1934a. Philp, 1933/1934b.

<sup>815</sup> Haldane, 1936c.

<sup>816</sup> Andersson-Kottö and Gairdner, 1936.

<sup>817</sup> Jenkin and Thomas, 1938/1939.

<sup>818</sup> Haldane, 1931/1932.

<sup>819</sup> Mather, 1933.

<sup>820</sup> Engledow, 1950/1951, 24. Bell, 1986, 218. Watkins and Cory, 1931/1932.

<sup>821</sup> Engledow, 1950/1951, 24.

<sup>822</sup> Morris and Richharia, 1937. Howard, 1938. Howard, 1939. Ellerton, 1939. Ellerton and Stebbins, 1938/1939.

<sup>823</sup> Black, 1933. Black, 1935.

rape and swedes.<sup>825</sup> Genetics research at the Welsh Plant Breeding Station was done with herbage and wetland grasses,<sup>826</sup> clover,<sup>827</sup> and *Solanum*, a genus which includes root vegetables, such as potatoes.<sup>828</sup> As Paolo Palladino has pointed out the types of plants researched at the three plant breeding institutes reflect the important agricultural crops in Scotland, Wales and England.<sup>829</sup> These organisms were all therefore of interest themselves, and thus physical models of groups low down the is-a hierarchy.

At Kew genetics research was done with domesticated garden plants such as *Antirrhinum vulneraria*<sup>830</sup> and *Saxifraga*,<sup>831</sup> and wild flowers such as *Ranunculus*<sup>832</sup> and *Centaurea*.<sup>833</sup> The organisms used at Kew reflect the location's status as a botanic garden.

Locations in the breeding setting mainly researched domesticated organisms of commercial value. The organisms tended to be used as models of groups low down the is-a hierarchy, rather than models of 'organisms'.

#### 4.3.3 Research Organisms in Conclusion

The settings therefore differed in type of organism and use of organism. Geneticists in the breeding setting tended to use domesticated organisms to obtain information about specific groups of domesticated organisms. Geneticists in the academic setting tended to use wild organisms to obtain information about organisms in general.

#### 4.4 Mice as Research Tools

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<sup>824</sup> Robb, 1932.

<sup>825</sup> Davey, 1931/1932.

<sup>826</sup> Jenkin, 1933/1934. Jenkin, 1935. Jenkin and Thomas, 1938/1939. Jenkin and Sethi, 1932.

<sup>827</sup> Williams and Silow, 1933. Williams, 1935. Williams, 1938/1939a. Williams, 1938/1939b. Williams, 1939.

<sup>828</sup> Ellison, 1936.

<sup>829</sup> Palladino, 2002, 47-48, 54.

<sup>830</sup> Marsden-Jones and Turrill, 1933.

<sup>831</sup> Marsden-Jones and Turrill, 1934.

<sup>832</sup> Marsden-Jones and Turrill, 1935.

<sup>833</sup> Marsden-Jones and Turrill, 1937.

In section 4.2 I showed that organisms were used at the DoZ/B as models of the type group 'organisms'. The information gained from a particular organism was thought to apply equally well to any other type. At the IAG, organisms were used either as models of groups low down the is-a hierarchy, or as instances of the type group 'organisms'. The information provided by the organisms were therefore not considered to apply equally well to any other type of organism. This difference led to a difference in the operational use of organisms at the two locations. In this section I study this difference with respect to mice. I show that at the DoZ/B, mice were treated as research tools by which to gain knowledge about processes or genetics that applied to organisms beyond the type group 'mice'. At the IAG, in contrast, mice were treated as dynamic, live organisms, which were used to gain knowledge about the genetics of 'mice'.

#### **4.4.1 Mice at the DoZ/B**

In this section I show that mice were seen and used, operationally, as tools by which to investigate genetics at the DoZ/B. This is seen mainly through the use of inbred mice at the Department. In this section I therefore also investigate why and how geneticists at the DoZ/B used inbred mice in their work.

##### **4.4.1.1 J.B.S. Haldane**

In this section I show that Haldane advocated the use of inbred mice because they allowed the genetic environment of an experiment to be controlled.

In 1933 Haldane published an article on the genetic study of cancer.<sup>834</sup> Haldane wrote that analysing the genetics of spontaneous cancer was difficult because death in a population of research organisms from causes other than cancer was unpreventable. The percentage of organisms that would develop cancer could not therefore be accurately obtained. However, cancer rates could be compared under different environmental conditions. Haldane stated:

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<sup>834</sup> Haldane, 1933.

“It is clear that a pure line (or the F1 hybrids of two pure lines) [F<sub>1</sub> hybrids are also genetically homogeneous] furnish ideal material for the determination of factors in the environment favourable or otherwise to the development of cancer.”<sup>835</sup>

The reason genetically homogeneous stocks were important for such work was that experimenters could vary just the environmental conditions. With genetically heterogeneous stocks both the environment and the genetics would vary. Haldane therefore advocated the use of inbred mice as tools to control the genetic environment of experiments.

While Haldane saw inbred mice as tools, he drew a distinction between inbred mice and the inanimate tools of other disciplines. In an article on pure lines, he stated:

“...there has been an unfortunate tendency to relax the inbreeding, as if its effects were irreversible, like those of repeatedly recrystallising a chemical substance...”<sup>836</sup>

Haldane therefore claimed that there was more invested in inbred mice than in chemical tools. He stated:

“...the interruption of genetical research involves throwing away the fruit of many years’ work, which is also true, for example, in bacteriology, but not in chemistry.”<sup>837</sup>

The reason for this was that if the research was interrupted, inbred organisms would not be maintained in their inbred state. The development of inbred organisms into useful tools was the result of many years work. Haldane’s group had carried out this work because they saw inbred organisms as useful tools for investigating genetics in general.

#### 4.4.2.2 Peter Gorer

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<sup>835</sup> Haldane, 1933, 266.

<sup>836</sup> Haldane, 1936b, 389.

<sup>837</sup> Haldane to Sir, 22 September 1939, f579, b45, s401D, RG1.1, RFA.

In this section I compare two of Gorer's papers to show how he used inbred mice as scientific tools in practice. In the first paper, Gorer describes experiments he performed with both heterogeneous and inbred mouse stocks. In the second paper, Gorer describes experiments he performed with just inbred mice. I show that the sole use of inbred mice allowed Gorer to greatly simplify his experiments. As such, Gorer used inbred mice as scientific tools to gain abstract knowledge about the genetics of serological reactions.

The main advantage Gorer found in using inbred mice was that because serological differences seemed to be entirely related to genetic differences, inbred mice did not vary serologically. Since immunisation experiments (described below) worked better if the blood of more than one mouse was used, inbred mice were a better scientific tool than heterogeneous mice.<sup>838</sup>

Absorption experiments could be done on individual mice. This type of experiment and agglutination experiments were therefore performed with the mixture of inbred and heterogeneous mice Gorer used in his first experiments.<sup>839</sup> In these experiments, Gorer obtained blood from the mice by cutting the end of their tails in preference to cardiac puncture. The latter was only used where necessary because it sometimes resulted in death and so prevented blood being obtained from that individual again.

To perform the agglutination experiment, Gorer mixed saline suspensions of blood with his own serum. These mixtures were then either left for an hour and a half, or centrifuged. They were then inspected for the extent of which the cells had clumped together.

Absorption experiments were performed by mixing the serum with the cells of one individual. This absorbed some of the antibodies. The blood of another mouse was then combined with the serum to see how the absorption had affected the serum's ability to agglutinate with the blood. Antigens in the absorbing blood would inactivate antibodies against them. The agglutination test with absorbed

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<sup>838</sup> Gorer, 1936a, 18.

<sup>839</sup> Gorer, 1936a.



serum therefore tested for antigens in the second lot of blood which were not present in the first.

Gorer performed very similar experiments with only inbred mice, which he published in the second paper I examine. In these experiments,<sup>840</sup> Gorer performed the same experiments as those described above, but with serum gained from immunised rabbits. Gorer immunised the rabbits with blood gained from the mice of one line by cardiac puncture. The blood could be pooled in this way because the mice were genetically homogeneous and thus, since serological variation was dependent upon genetic variation, serologically homogeneous. The rabbits produced serum containing antibodies to the antigens in the blood they were injected with. The serum was then used for agglutination and absorption experiments as described above.

The use of serum from immunised rabbits was beneficial because Gorer showed that no antigenic differences were detected between the mouse lines with normal rabbit serum. This meant that any differences seen were due to the immunisation process. This process added antibodies against the blood the rabbit was injected with into its serum. If the blood of one line agglutinated with the serum gained from immunised rabbits more strongly than with normal rabbit serum, it was thought to share antibodies with the line whose blood was used to immunise the rabbit. If absorption of the serum with another line prevented agglutination, all three lines shared the antigen.

A direct comparison of the antigens of three lines was therefore possible using the immunisation technique. Only two lines could be directly compared without it. The technique itself required the lines to be inbred. The use of inbred lines was therefore beneficial for identify serological differences. They were also useful for analysing the genetics behind these differences, because the genes of each line were known to be homozygous.

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<sup>840</sup> See Gorer, 1937a.

In his next paper, Gorer described how he had crossed inbred albino and black mice to form an F<sub>1</sub> generation. These were then interbred or back-crossed to inbred black mice. The mice of each generation were tested by both the agglutination and absorption method for their reaction to anti-black sera. The percentage of individuals in each generation to react to the sera was then compared to the percentage of individuals that would be expected to be homozygous for the black allele at any location, heterozygous at any location and homozygous for the albino allele at any location. The genetic analysis depended upon Gorer's ability to give these percentages. Since the mice crossed to form the F<sub>1</sub> generation were homozygous at every gene locus, this greatly eased the analysis Gorer had to do.

Gorer therefore used inbred mice as genetic tools to extend his ability to analyse serological differences and to simplify his investigation of the genetics behind such differences.

#### 4.4.1.3 Hans Grüneberg

Just as Gorer used inbred mice as a tool to study the genetics of serological reactions, Grüneberg used heterogeneous mice as a tool to study the order of the genes for shaker, albinism and pink eye on a chromosome. Thus, the difference between the departments was not solely due to their differential use of inbred mice.

Grüneberg mapped the three genes by calculating the frequency at which crossing-over occurred between them. To conduct the experiment Grüneberg created mice with the genotypes  $\begin{matrix} \text{(sh, p, +)} \\ \text{( +, +, d)} \end{matrix}$  and  $\begin{matrix} \text{(sh, p, a)} \\ \text{(sh, p, a)} \end{matrix}$ .<sup>841</sup>

He then crossed female  $\begin{matrix} \text{(sh, p, +)} \\ \text{( +, +, d)} \end{matrix}$  and male  $\begin{matrix} \text{(sh, p, a)} \\ \text{(sh, p, a)} \end{matrix}$  mice. One of the mice used in the

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<sup>841</sup> sh = shaker, p = pink-eye, + = wild-type, d = extreme dilution allelomorph of albino, a = albino.

cross was homozygous recessive for the three genes of interest, so Grüneberg would know the alleles inherited from that parent and they would not be seen in the offspring unless the other parent also provided an allele for the character of interest. The genetics of the other mouse crossed were set up so that all the alleles were present, but one was on a different chromosome. Extreme dilution would not be inherited with either of the other alleles unless crossing-over occurred, similarly shaker and pink-eye would always be inherited together in the absence of crossing over. By producing a large number of offspring Grüneberg could therefore see how frequent crossing-over was between different genes. The more frequent it was the further apart the genes were supposed to be on the chromosome.

Grüneberg therefore designed the genetics of the mice so he could use them to discover the locations of the genes with respect to each other. The mice he began with were therefore transformed into scientific tools before he used them for his investigation. Furthermore, the importance of Grüneberg's work was that it began the process of mapping the mouse chromosomes.<sup>842</sup> Mapping was the only way of judging whether genes producing the same phenotypic effects did so because they were allelomorphous or because they affected the same developmental process. This work therefore helped to make mice a more useful genetic tool.

#### **4.4.1.4 Mice at the DoZ/B in Conclusion**

At the DoZ/B mice were chosen as appropriate organisms with which to investigate various genetic problems. Haldane advocated their use to investigate the genetics of cancer. Gorer used them to investigate the genetics of serological reactions. Grüneberg tried to further develop them into more useful tools for physiological research. In Haldane and Gorer's cases, the problem pre-existed the choice of organism and had implications beyond the type group 'mice'. Haldane explicitly referred to the applicability of results with mice to human

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<sup>842</sup> Lewis and Hunt, 1984, 232.

cancer.<sup>843</sup> Gorer's work was originally going to be conducted with fowl, and of this work he wrote:

“..it is hoped that the results will be of value to human geneticists; in addition it is possible that light may be thrown upon various problems of immunology.”<sup>844</sup>

The proposed work with fowl was funded, in part, by the Medical Research Council, on recommendation of the human genetics committee.<sup>845</sup> Mice were therefore used as tools at the DoZ/B to investigate problems that existed beyond mice. While the geneticists did not forget they were live, mice were used to control genetic variables, rather than to investigate the complexity of life.

#### **4.4.2 Mice at the IAG**

Mice were operationally used very differently at the IAG from the DoZ/B. They were not portrayed as genetic research tools but as live organisms whose genetics were of interest. This can be seen primarily through three papers Crew published on the genetics of mice.

##### **4.4.2.1 The Genetics of Mice**

In 1931 Crew and Mirskaia published an article on the development of hairlessness in mice.<sup>846</sup> Stocks of hairless mice were kept in the Institute from 1925. In 1927 Crew established that the character was due to a single recessive gene, but the linkage of the gene was established by American geneticists. Until 1928, it was only possible to maintain the stock because hairless young tended to die, hairless mothers could not rear young and haired males would not breed with hairless females. Hairless mice were therefore far from a useful scientific tool. Their behaviour and their physiology made them hard to breed and therefore hard to do genetic tests with.

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<sup>843</sup> Haldane, 1933, 266.

<sup>844</sup> Application by Dr P.A. Gorer, 20 January 1933, folder FD1/3287, MRC papers.

<sup>845</sup> Minutes, 28 April 1933, folder FD1/3287, MRC papers.

<sup>846</sup> Crew and Mirskaia, 1931.

Crew and Mirskaia noticed that the relationship between the recessive gene for hairlessness and other characters related to hairlessness was not simple. They explained this with reference to the pleiotropic action of the hairlessness gene and its interaction with other genes. This explanation led them to begin to trace the development of the hairlessness character in mice. For this they looked at the histology of the mice's skin and considered the effect of hormones on normal metabolism.

Crew's research on 'waved' mice shows similarities to that described above. In 1933, he published a short paper<sup>847</sup> describing the genetics and temporal development of the trait. The paper begins by describing the origin of the mice with the phenotype. The temporal development of the phenotype is then described. Crew next describes the crosses he performed to establish the genetics of the trait. He firstly crossed normal and waved mice and then inter-crossed the offspring and compared the number of waved mice in the F<sub>1</sub> generation with that expected if the phenotype was controlled by a single, recessive gene. He then crossed waved mice and compared the number of waved and normal mice with that expected if the trait was due to a single, recessive gene. He noted that the sex ratio was slightly odd, but concluded that the gene was nevertheless autosomal. He then ended the paper by drawing attention to the similarity between this phenotype and the 'curly coat' phenotype in rats. Crew did not establish the linkage of the gene. Instead, he sent some of the mice to the American geneticist, L.C. Dunn, to establish the gene's linkage group.<sup>848</sup> As for the 'hairless' trait, the simple genetics were determined by Crew, but the linkage group of the gene was determined by other geneticists. This suggests that it was the phenotype, not the gene for the trait that was of interest to Crew.

The final paper on mouse genetics Crew published during the 1930s was on the trait 'Rex' and was co-authored with Charlotte Auerbach in 1939.<sup>849</sup> This paper shows many similarities with those described above. Again the phenotype and simple genetics of the trait were described. However, in this paper the trait was

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<sup>847</sup> Crew, 1933.

<sup>848</sup> Crew to Dunn, April 1, 1933, folder Crew, F.A.E., Dunn papers.

<sup>849</sup> Crew and Auerbach, 1939.

tested for its identity with another character, Caracul. Crew and Auerbach did this by crossing homozygous Rex and inbred Caracul mice and mating the offspring to inbred mice that were non-Rex, non-Caracul. They then compared the ratio of phenotypes in the F<sub>2</sub> with those expected if the two genes were allelomorphous. In finding that the two traits were not genetically identical, the pair concluded that they probably affected the same developmental process.

#### **4.4.2.2 Mice at the IAG in Conclusion**

At the IAG mice were not treated as genetic research tools. They were not used to investigate physiological phenomena such as the development of cancer or serological differences. Instead, they were used to investigate the genetics behind traits that arose in them and physiological processes were invoked to explain these traits. Crew did not establish the linkage group of the genes he studied or their linkage values with respect to other genes. This, as seen for Grüneberg, would have helped to make mice a more useful genetic tool. While Crew does not appear to have seen mice as a research tool, he saw them as live organisms. Thus, in two of the three papers studied he referred to the action of genes on the development of the mice.

#### **4.4.3 Mice as Research Tools in Conclusion**

In section 4.4 I have shown that mice were seen as research tools at the DoZ/B, which could be used to investigate problems that applied to organisms beyond the type group 'mice'. At the IAG, in contrast, mice were seen as live organisms that were of interest in themselves.

These differences can be explained in two ways. Firstly, by the fact that the problem came first at the DoZ/B. Mice were used in the research because they were considered to be the right tool, epistemologically, for the job. At the IAG the organism came first and created jobs. The geneticists at the IAG therefore reacted to occurrences in their mouse stocks, rather than pro-actively sought methods by which to investigate problems of interest. Secondly, genetics was performed alongside physiological experiments at the IAG. These relied upon the

fact that mice were live, holistic organisms. Finally, genetics was applied to livestock at the IAG. This demonstrated the difficulty of applying the genetic principles found with one organism to another. This meant that it was not thought possible to use mice as a model of 'organisms' at the IAG. If this was not possible, mice could not be research tools to find out about 'organisms'.

## 4.5 Conclusion

Choice of research organism was a good indicator of settings during the 1930s. Animals tended to be wild or artificial in the academic setting and domesticated in the breeding setting. However, plants tended to be domesticated regardless of the setting they were used in.

Domesticated organisms were usually used as physical models of groups low down the is-a hierarchy. This was not always true, however, as shown by Koller's use of cats and dogs for comparative cytology. Nevertheless, the breeding setting and botany departments in the academic setting tended to use the organisms they studied as physical models of groups low down the hierarchy. Where organisms were used to provide information about 'organisms', they were usually used as instances of 'organisms', rather than as models of 'organisms'. This was the opposite of zoology departments in the British academic setting. Despite the common use of wild animals, organisms tended to be used to provide information about 'organisms' and were used just as commonly as models of 'organisms' as instances. Some organisms were used as physical models of groups low down the is-a hierarchy, however, as shown by Grüneberg's work on linkage in artificial mice.

The other distinction between the breeding and academic settings was in the whether organisms were used as research tools or not. The DoZ/B used mice as tools to investigate problems that applied to groups beyond the type group 'mice'. The IAG did not use mice as genetic tools, but investigated the genetics of phenotypes that arose in their stocks. This difference can be explained by the fact that a variety of approaches were taken at the Institute to improving the

breeding of domesticated animals. The different approaches emphasised the point that animals are live organisms, which differ in their genetics.

As well as adding to my thesis regarding the distinction between settings, this chapter adds to our understanding of model organisms and the 'right tool for the job' thesis. It demonstrates that the use of research organisms as model organisms<sup>850</sup> is a specific example of organisms being used to model type groups, and that the latter almost always occurs in genetic research. almost always occurs. My work also shows that organisms do not have to be used as either the models of groups lower down the is-a hierarchy or as a model of 'organisms'. They can also be used as instances of 'organisms'. This was the case for Koller's comparative cytogenetical studies in the breeding setting and Grüneberg's developmental studies in the academic setting.

The 'right tool for the job' thesis is demonstrated in this chapter, in all three of its incarnations. For example, sociologically, *Drosophila* was the right tool for academic genetics activities at both the IAG and the DoZ/B because both locations had to provide for students and *Drosophila* had a fast reproductive turnover.<sup>851</sup> It was also inexpensive, which was especially important at the DoZ/B, which had few sources of funding. Haldane argued that scientifically, inbred mice were the right tool for investigating the genetics of cancer. The organism also gave rise to the job, making it the right job for the tool, in the case of Grüneberg's developmental genetics work.<sup>852</sup> A mutation arose in the DoZ/B's mouse stock that affected the developmental process, suggesting that the mice were used to investigate the genetics of development.

As the decade advanced Haldane began to advocate the use of wild animals because he was concerned about the effects of domestication on the results obtained. He was thus concerned that artificial animals were not good physical

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<sup>850</sup> In Creager's first sense (the findings apply to organisms beyond those studied). Creager, 2002, 4-5.

<sup>851</sup> This has been discussed by Kohler, 1994, 33-37. Sociological 'rightness' is discussed in Clarke (Adele), and Fujimura, 1992b.

<sup>852</sup> Lederman and Burian, 1993 discuss the difference between scientifically right and organisms giving rise to jobs.



models of 'organisms'. This move demonstrates the distinction Lynch<sup>853</sup> has made between naturalistic and analytic animals. However, it shows that naturalistic animals could still be used analytically. Haldane's concern with domestication also shows that the concern Löwy and Gaillièrè<sup>854</sup> identified amongst cancer researchers regarding the artificiality of inbred mice was more widespread during the 1930s than previously thought. The concern about artificiality did not just apply to inbred animals but to artificial and domesticated animals. It was a concern not just for cancer researchers but for epistemologically cautious geneticists themselves.

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<sup>853</sup> Lynch, 1988, 267.

<sup>854</sup> Löwy and Gaillièrè, 1998.

## **Chapter Five**

### **Problem Choice**

#### **5.1 Introduction**

In this chapter I study another characteristic of genetics: research problem. I investigate the differences between research problems tackled at the DoZ/B and the IAG and consider how representative these were of differences between their respective settings. Finally, I investigate a research area studied at both the locations and show that even in that case the focus of the investigations differed.

I begin, in section 5.2, by investigating the variety of research problems at the two locations. I show the DoZ/B changed focus from a mixture of physiological and population genetics problems in the early 1930s to focusing on population genetics by the end of the 1930s. These problems were all academic activities. At the IAG a variety of breeding and academic activities took place. These varied from analysing and improving agricultural breeds, to physiological and transmission genetics research. The IAG therefore embraced a wider range of problems into its definition of genetics.

Next, in section 5.3, I demonstrate that these findings were representative of the academic and breeding settings. I show that the main types of research conducted in academic zoology departments were transmission and population genetics. In botany departments the main type of research was cytogenetics. These are academic activities. In the breeding setting the research tended to be transmission genetics and cytogenetics. The academic setting was synthetic in its approach to genetics. This was less true of the breeding setting, which used genetics and cytology simultaneously as separate approaches to the investigation of breeding.

Finally, in section 5.4, I investigate the specific problems studied at the two locations for a research area they had in common: chromosomal studies. I distinguish between three kinds of chromosomal problems: genetic, cytogenetic and cytological. I show that geneticists at the DoZ/B tended to study genetic

problems, whereas the geneticists at the IAG studied genetic, cytogenetic and cytological problems.

## 5.2 Problem Choice

In this section I compare the types of problem tackled at the DoZ/B and the IAG. Problem choice is influenced by many factors. In this section I investigate how those factors influenced problem choice at the two locations.

### 5.2.1 Problem Choice at the DoZ/B

In this section I show that problem choice at the DoZ/B was primarily driven by Haldane. He had a strong vision of genetics at the location. However, this vision was dependent upon the group's ability to carry out the research. This in turn was influenced by the funding they received. Haldane's vision was also sometimes set aside as contingences provided new opportunities for research.

#### 5.2.1.1 1933

In 1932 Haldane wrote to the mouse geneticist, L.C. Dunn, of his plans for research. He planned to conduct linkage experiments with mice and to compare inbred lines for physiological, pharmacological and serological differences. With *Drosophila* he planned to conduct experimental population studies.<sup>855</sup> In this section I demonstrate the importance of Haldane's vision to the work conducted at the DoZ/B in 1933.

By the end of 1933 three of these lines of work were underway. Linkage studies were being conducted on the 'wavy' gene in mice and mice were being bred with the aim of obtaining triple recessive mice for pink eye, shaker and albino/extreme dilution.<sup>856</sup> Once these had been obtained linkage studies between

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<sup>855</sup> Haldane to Dunn, October 10, [1932], folder Haldane, J.B.S., Dunn papers.

<sup>856</sup> Haldane to Dunn, July [1933], folder Haldane, J.B.S., Dunn papers. The genes being tested are stated in Haldane to Dunn, October 10, [1932], folder Haldane, J.B.S., Dunn papers. Here, however it says "white". White describes the phenotypic effect of the alleles. The alleles used were albino and extreme dilution. The latter was used as well as albino because albino produces

the three genes could begin. The importance of this work, as discussed in section 5.4, was that it began the process of mapping the mouse chromosomes. This was important for physiological genetics, as it enabled allelomorphs to be distinguished from alleles that affected the same physiological process. This work therefore fitted into Haldane's physiological genetics programme.

In 1933 Haldane began supervising work on serological differences in fowl at the JI, funded by the Medical Research Council.<sup>857</sup> However, the work did not progress very far. The project appears to have changed to looking at serological differences between strains of mice at UCL at the end of 1933.<sup>858</sup> The project thus changed towards Haldane's vision of genetics and moved location.

In 1933 Haldane also began the experimental population studies he had planned. During that summer Haldane wrote that the British fruit fly, *Drosophila subobscura*, was being inbred in the department to see what mutations existed in the wild.<sup>859</sup> This work showed how much genetic variation existed in wild populations and could be used to explain the number of similar species.<sup>860</sup>

One other piece of work, which probably began at the end of 1933, did not fit Haldane's vision particularly well. This was chromosomal genetics using *Drosophila*. In August 1933 Philip joined the department and worked on crossing over in *Drosophila*.<sup>861</sup> Philip moved to the department by invitation from Haldane. He invited Philip because she was a young German Jewish geneticist, whose future in Germany looked doubtful.<sup>862</sup> Her move to the department was not therefore due to her ability to conduct any particular type of research. The studies she performed on crossing-over probably reflected her background as a

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pink eyes as well as the allele 'pink eye', and thus the presence of the latter cannot be determined when albinism is present. Extreme dilution is allelomorphic to albino but it does not produce pink eyes, so the presence of the pink eye allele can be determined in its presence. (Grüneberg, 1935a, 158-159).

<sup>857</sup> "GTI" to Gorer, 3 May 1933, folder FD1/3287, MRC papers. Gorer to "Sir", 8 May 1933, folder FD1/3287, MRC papers.

<sup>858</sup> Gorer to "Sir", 14 June 1934, folder FD1/3287, MRC papers. Miller's diary, March 14-15, 1934, RG 12.1, RFA.

<sup>859</sup> Haldane to Dunn, July [1933], folder Haldane, J.B.S., Dunn papers.

<sup>860</sup> "Work in Progress in de [sic] Department of Genetics. University College, London," f578, b45, s401D, RG1.1, RFA.

<sup>861</sup> Miller's diary, March 14-15, 1934, RG12.1, RFA.

<sup>862</sup> See Chapter Two (section 2.2.2) for further details.

student of the *Drosophilist* Curt Stern.<sup>863</sup> The work had some evolutionary significance, however, and was therefore probably not discouraged by Haldane.

During 1933 the genetics research carried out at the DoZ/B was heavily influenced by Haldane's interests in physiological and population genetics. In 1932 Haldane had published a book on population genetics<sup>864</sup> and prior to joining the DoZ/B he had worked part-time at the Biochemistry Department at Cambridge University.<sup>865</sup> These interests therefore reflected Haldane's past, which as demonstrated in Chapter Two (section 2.2) coincided well with Watson's interest in the department.

#### 5.2.1.2 1934

During 1934 the work already begun in the department expanded. In this section I show that the areas of expansion were due to the training and funding of Haldane's research team. New projects were also added to the research programme. I show that some of these, such as physiological genetic projects, were part of Haldane's research plan. Others, such as developmental genetics, were not and were conducted because contingences presented the opportunity for their study.

In 1934 three new types of work began in the department. The first compared haemoglobin in different strains of inbred mice.<sup>866</sup> Physiological differences between strains therefore began to be studied in the department as Haldane had planned. The other two projects had not formed part of Haldane's vision. One was theoretical research on inbreeding and human linkage, conducted by Haldane.<sup>867</sup> Though it had not been part of his original research plan, the work clearly reflected Haldane's interests. The other new area of research was developmental genetics. In 1934 a mutation arose in the mouse stocks that

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<sup>863</sup> *The Eugenics Review* 56: 66.

<sup>864</sup> Haldane, 1932.

<sup>865</sup> Pirie, 1966, 220-221.

<sup>866</sup> Miller's diary, October 22, 1934, RG12.1, RFA.

<sup>867</sup> Summary of work in progress, 3 October 1934, f578, b45, s401D, RG1.1, RFA. Haldane, 1936b.

affected the development of mice.<sup>868</sup> This contingency provided the opportunity to investigate how genes affect development. The opportunity was taken up by Grüneberg, who had a prior interest in morphological genetics.<sup>869</sup>

As well as these new projects, research on population genetics broadened in scope. Koller began to study the cytology of inter-racial hybrids.<sup>870</sup> As described in section 5.4, this work compared the chromosomes of different races and explained the sterility that arose between them, leading to speciation. The problem of speciation was also tackled by studying preferential mating.<sup>871</sup> The flow of genes through a population was studied by release and capture studies of *Drosophila* at two separate locations.<sup>872</sup> The work that had been started on the mutations found in wild populations also continued.<sup>873</sup> However, inbreeding could not reveal sex-linked mutations. This meant the homology of the sex chromosomes could not be analysed. Christie therefore began studying the mutations produced by X-ray radiation,<sup>874</sup> which enabled genes on the sex chromosomes to be identified.

The chromosomal genetics work of the department also expanded. As Christie's X-ray experiments continued, an inversion arose in the X-chromosome of *Drosophila melanogaster*. This contingent event led Grüneberg and Koller to study the inversion.<sup>875</sup> Koller also began to study meiosis in rats and monkeys. This work reflected Koller's training as a cytogeneticist. At the time he was boarding with the cytologist, Cyril Darlington.<sup>876</sup> He therefore had plenty of opportunity to discuss Darlington's cytogenetic ideas (discussed in section 5.4), which Koller's studies of meiosis helped to clarify. Philip's work on crossing

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<sup>868</sup> Miller's diary, October 22, 1934, RG12.1, RFA.

<sup>869</sup> Summary of work in progress, 3 October 1934, f578, b45, s401D, RG1.1, RFA. Miller's diary, October 22, 1934, RG12.1, RFA. Grüneberg, 1935c, 321. Lewis and Hunt, 1984.

<sup>870</sup> Summary of work in progress, 3 October 1934, f578, b45, s401D, RG1.1, RFA.

<sup>871</sup> Miller's diary, October 22, 1934, RG12.1, RFA. "Work in Progress in de [sic] Department of Genetics. University College, London," f578, b45, s401D, RG1.1, RFA.

<sup>872</sup> Summary of work in progress, 3 October 1934, f578, b45, s401D, RG1.1, RFA. Miller's diary, October 22, 1934, RG 12.1, RFA. Miller's diary, September 26, 27, 28, 1935, RG12.1, RFA. Gordon, 1936.

<sup>873</sup> Summary of work in progress, 3 October 1934, f578, b45, s401D, RG1.1, RFA. Miller's diary, October 22, 1934, RG12.1, RFA.

<sup>874</sup> Miller's diary, October 22, 1934, RG12.1, RFA. Christie, 1939/1940.

<sup>875</sup> Summary of work in progress, 3 October 1934, f578, b45, s401D, RG1.1, RFA. Grüneberg, 1935b.

<sup>876</sup> Miller's diary, October 22, 1934, RG12.1, RFA.

over in *Drosophila* continued.<sup>877</sup> The linkage studies on mice that had begun in 1933 were also continued throughout 1934 and were expanded to include linkage in humans.<sup>878</sup>

One departmental project that waned during 1934 was the serological comparison of different strains of mice. This was conducted by Peter Gorer. In 1934 Gorer joined the Lister Institute part-time and conducted his experimental work there, while retaining his affiliation with UCL.<sup>879</sup> The DoZ probably influenced the theoretical framework of this work, but the actual experiments were conducted elsewhere.

Haldane's vision of genetics at the DoZ/B was therefore fulfilled, and exceeded, during 1934. This was possible because there was a large increase in the number of genetic researchers at the department. Some of these researchers had previous training and experience. Their research tended to reflect, at least in part, their backgrounds. For example, Koller worked on cytogenetic problems and Philip worked on crossing-over in *Drosophila*. Many of the researchers were PhD students or had no funding and were therefore in an unstable situation (as described in Chapters Two and Three, sections 2.2 and 3.3.1). As discussed in Chapter Four (section 4.5) *Drosophila* was a good organism for students due to its inexpensiveness and fast reproductive turn-over. This argument applies equally well for researchers on temporary or no funding. *Drosophila* is not as suitable as mice for physiological genetics; however, it is more suitable for population genetics. This explains why population genetics expanded so much during 1934 compared to the other areas of Haldane's vision.

### 5.2.1.3 1935

During 1935 the work of the department changed little. Some change occurred due to staff losses, but since the programme reflected Haldane's vision there was little impetus for change.

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<sup>877</sup> Summary of work in progress, 3 October 1934, f578, b45, s401D, RG1.1, RFA. Philip, 1935.

<sup>878</sup> Summary of work in progress, 3 October 1934, f578, b45, s401D, RG1.1, RFA.

<sup>879</sup> Medawar, 1961, 97. Summary of work in progress, 3 October 1934, f578, b45, s401D, RG1.1, RFA. Gorer, 1936a, 17, 30.

Two new problems began to be tackled during 1935. The first involved collaboration between Haldane and the Royal Eastern Counties' Institution's L. Penrose, to research the rate of mutation of a human gene.<sup>880</sup> This related to the work Haldane was already conducting on human linkage. He, and his collaborator, Julia Bell, investigated whether haemophilia was due to mutation or crossing over.<sup>881</sup>

The other new project was the investigation of different organisms as material for genetics work. This extended from considering their suitability to understanding the biology of species already used and how to best keep and breed them.<sup>882</sup> This project possibly arose because Haldane realised that he had a niche in studying *Drosophila sub-obscura*<sup>883</sup> (see Chapter Four, section 4.2.2.2) and wondered if there were any other suitable organisms not already being used for genetics.

Work on population genetics remained the top priority in the department. The research being done on mate selection, release and capture experiments, the mutations found in wild populations and those caused by X-rays, all continued. The research on mutations found in natural populations was extended to wild mice. Haldane claimed that the work with mice was important not just for population genetics but because it may throw light on the effect of inbreeding in humans.<sup>884</sup> The one population genetics project to be discontinued in 1935 was the cytological study of interracial hybrids.<sup>885</sup> This was discontinued because Koller left the department and no-one else was trained in the use of cytological methodology.

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<sup>880</sup> "Work in Progress in de [sic] Department of Genetics. University College, London," f578, b45, s401D, RG1.1, RFA. This work had not been mentioned in any correspondence before this one in October 1935. However it is possible that it was begun before 1935, since Haldane published a paper on the mutation rate of a human gene in October 1935 (Haldane, 1935).

<sup>881</sup> Tisdale's diary, October 21 and 22, 1935, f578, b45, s401D, RG1.1, RFA.

<sup>882</sup> "Work in Progress in de [sic] Department of Genetics. University College, London," f578, b45, s401D, RG1.1, RFA.

<sup>883</sup> Projects for Research in Animal Genetics, December 1935, f578, b45, s401D, RG1.1, RFA.

<sup>884</sup> "Work in Progress in de [sic] Department of Genetics. University College, London," f578, b45, s401D, RG1.1, RFA. Grant-in-aid 35254, f578, b45, s401D, RG1.1, RFA.

<sup>885</sup> This presumably continued until Koller, who was conducting the work, (Summary of Work in Progress, 3 October 1934, f578, b45, s401D, RG1.1, RFA) left the department in March 1935. (Miller's diary, March 13, 1935, RG12.1, RFA. Koller to Darlington, 29 March 1935, folder J.123, box c.110, Darlington papers.) It was not going on in October 1935: "Work in Progress in de [sic] Department of Genetics. University College, London," f578, b45, s401D, RG1.1, RFA.



The chromosomal research conducted in the department was also partly affected by the loss of Koller. His research on meiosis was discontinued.<sup>886</sup> Grüneberg's investigation of the inversion in the X-chromosome was continued.<sup>887</sup> However, and at some point during 1935 or 1936, the chromosome re-inverted. This contingent event enabled a complete re-inversion to be investigated both by Grüneberg<sup>888</sup> and cytologically by C.W. Emmens.<sup>889</sup> Philip's work on crossing over also continued.<sup>890</sup> The linkage studies with pink eye, shaker and albino/extreme dilution also continued and the results were used to investigate interference to crossing-over.<sup>891</sup>

Developmental genetics work continued into the same gene as studied in 1934, which caused phenotypic effects ranging from a lack of yellow pigmentation in the coats of the mice, to a failure of the teeth to erupt, to premature death.<sup>892</sup>

Gorer continued to be affiliated with UCL and thus his work on the serology of mouse strains continued to be part of the department's programme of work. He also compared the susceptibility of different strains to infection. Although Haldane listed this work as part of the department's programme in 1935 it probably should not be considered as such. Gorer published this work jointly with two researchers from the Lister Institute and the affiliation stated was solely the Lister Institute.<sup>893</sup>

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<sup>886</sup> "Work in Progress in de [sic] Department of Genetics. University College, London," f578, b45, s401D, RG1.1, RFA.

<sup>887</sup> "Work in Progress in de [sic] Department of Genetics. University College, London," f578, b45, s401D, RG1.1, RFA.

<sup>888</sup> Grüneberg, 1937.

<sup>889</sup> Emmens, 1937.

<sup>890</sup> "Work in Progress in de [sic] Department of Genetics. University College, London," f578, b45, s401D, RG1.1, RFA.

<sup>891</sup> "Work in Progress in de [sic] Department of Genetics. University College, London," f578, b45, s401D, RG1.1, RFA. Gruneberg, 1936d.

<sup>892</sup> "Work in Progress in de [sic] Department of Genetics. University College, London," f578, b45, s401D, RG1.1, RFA. Grüneberg, 1935c.

<sup>893</sup> Schütze, Gorer and Finlayson, 1936.

In 1935 the work on physiological differences between pure lines of mice was discontinued.<sup>894</sup> In March 1935 the RF official, H.M. Miller, recorded that no results had been gained from this work.<sup>895</sup>

During 1935 the work of the Department therefore changed little. The few changes there were, were caused by staff changes, or few results being gained. Also, new organisms were investigated to assess their utility for research and to identify new research problems.

#### 5.2.1.4 1936/1937

Over the course of 1936/1937 a number of projects came to an end and a number of staff left the department. At this time some research areas underwent renewal; others were allowed to lapse. Population genetics became established as the major field of work in the department. Developmental genetics and human genetics became established as the department's other interests.

During 1936/1937 the major field of work in the department was clearly established as population genetics. Yet this work also underwent a form of closure and renewal in this period. The work on mate selection ended. The last mention of the work I have found is in February 1936<sup>896</sup> and the last mention of Minns, who conducted the work, is in June 1936.<sup>897</sup> The release and capture experiments with *Drosophila* also drew to an end. The experiments were part of Haldane's planned work in December 1935<sup>898</sup> but they were not mentioned again and Gordon, who conducted the experiments, left the department in August 1937.<sup>899</sup> Christie also finished his PhD on the effect of X-rays in early 1936.<sup>900</sup> The discontinuation of this work therefore seems to be due to the loss of a number of staff members. The work on inbreeding wild organisms to see what

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<sup>894</sup> This work is not mentioned in Haldane's "Work in Progress in de [sic] Department of Genetics. University College, London," f578, b45, s401D, RG1.1, RFA.

<sup>895</sup> Miller's diary, March 13, 1935, RG12.1, RFA.

<sup>896</sup> Haldane to Tisdale, f579, b45, s401D, RG1.1, RFA.

<sup>897</sup> Tisdale's diary, June 12, 1936, f579, b45, s401D, RG1.1, RFA.

<sup>898</sup> "Projects for Research in Animal Genetics," f578, b45, s401D, RG1.1, RFA.

<sup>899</sup> Gordon, Spurway, Street, 1939, 38. Tisdale's diary, June 27-28, 1937, f39, b3, s405D, RG1.1, RFA. Hogben to Tisdale, September 28, 1937, f106 NS Scotland, b10, s1.1D, RG6.1, RFA.

<sup>900</sup> See chapter two (section 2.2.5) for further details. Christie, 1939/1940.

mutations were found was, however, continued. Work on inbreeding wild mice was continued<sup>901</sup> and extended to beetles.<sup>902</sup> This work was also continued in *Drosophila*.<sup>903</sup> One project began and ended in this period. This was the Rockefeller Fellow, L. Csik's, work on the effects of oxygen deprivation on *Drosophila*. Csik looked at these differences within and between species and investigated whether it caused mutations.<sup>904</sup> Such work could have explained the different mutability of species and thus different evolutionary patterns.

The department's second area of interest was established in 1936/1937 as developmental genetics. In 1936 the department's work on the grey-lethal gene, discovered in 1934, was extended to an investigation of the affected animals' biochemistry. This work was done by a collaborator at the Cambridge biochemical laboratories.<sup>905</sup> In 1937 the work, which could easily have come to a natural end when the investigation of grey-lethal finished, became slightly better established as Grüneberg discovered a lethal gene in rats.<sup>906</sup> This contingency, together with the training Grüneberg had gained from his previous work, kept developmental genetics a going concern of the Department. One of the department's visitors, Sara Bedichek, also investigated developmental genetics in *Drosophila* by looking at intersexes.<sup>907</sup>

Human genetics was the other interest the department retained. Haldane continued his research on human genetics by studying linkage with colour blindness throughout 1936 and 1937<sup>908</sup> and studied the number of lethal genes in man.<sup>909</sup> The continuation of these studies reflected Haldane's interests.

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<sup>901</sup> "Projects for Research in Animal Genetics," f578, b45, s401D, RG1.1, RFA.

<sup>902</sup> Miller's diary, April 17-22, 1937, RG 12.1, RFA. Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL. See also Philip, 1938.

<sup>903</sup> Gordon, Spurway, Street, 1939, 38.

<sup>904</sup> Miller's diary, November 16-17, 1936, RG12.1, RFA.

<sup>905</sup> Watchorn to Grüneberg, 16 March 1936, folder Wae-Way, b17, Grüneberg papers. See also Watchorn, 1938 and Grüneberg, 1938b.

<sup>906</sup> Miller's diary, April 12, 1937, RG12.1, RFA. Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL. See also Grüneberg, 1938a.

<sup>907</sup> Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL.

<sup>908</sup> Haldane to Tisdale, January 27, 1936, f579, b45, s401D, RG1.1, RFA. Miller's diary, November 16-17, 1936, RG12.1, RFA. Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL.

<sup>909</sup> Miller's diary, January 28-29, 1937, RG12.1, RFA.

Some other research was also conducted in the Department during this period. As discussed in Chapter Four (section 4.2.2.1) Haldane became interested in the effects of domestication in 1936. In that year experimental work was done comparing haemoglobin in wild and tame mice.<sup>910</sup> Haldane also considered the problem of how much heterozygosity would theoretically be expected in a pure line.<sup>911</sup> This helped him to assess the limits of using inbred mice as a homogeneous genetic tool as discussed in Chapter Four (section 4.4.2.1). Some exploration of new material for genetic investigation also continued. In 1937 work was being done in the department on the genetics of the ray, *Lebistes*.<sup>912</sup>

The rest of the research in the department was discontinued. Grüneberg and Emmens's work on the inversion of a chromosome in *Drosophila* appears to have finished with the publication of their papers in 1937.<sup>913</sup> There is no evidence of work on crossing over continuing into 1936 and 1937, except Haldane's plan for it to.<sup>914</sup> This was probably because the opportunity that contingency had given them had been fully exploited by 1937. Linkage work with mice was also discontinued. The last paper on mouse linkage was published by Grüneberg and Haldane in 1937/1938.<sup>915</sup> This work also followed up on oddities previously found and thus probably came to a natural end. Work on the serological differences between lines of mice completely moved to the Lister Institute when Gorer was employed there full-time in 1936.<sup>916</sup>

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<sup>910</sup> Miller's diary, November 16-17, 1936, RG12.1, RFA.

<sup>911</sup> Haldane, 1936b.

<sup>912</sup> Miller's diary, April 17-22, 1937, RG12.1, RFA. Haldane to Tisdale, 6 December 1937, b26, Haldane papers, UCL.

<sup>913</sup> Grüneberg, 1937. Emmens, 1937. Muller and Grüneberg corresponded over this phenomenon. The last letter between them on this subject is Muller to Grüneberg, 11 February 1937, folder Mou-Mu, b11, Grüneberg papers. Haldane mentioned it as part of Grüneberg's ongoing work in December 1937 however. This may have been due to the recent publication of the work or the work may have continued into the early parts of 1938. The former seems more likely. Haldane included the work of Sara Bedichek in this letter despite her return to America in August 1937. (Grüneberg to Dunn, 24 August 1937, folder Grüneberg, Hans III, Dunn papers.)

<sup>914</sup> "Projects for Research in Animal Genetics," f578, b45, s401D, RG1.1, RFA. The work was certainly not mentioned as part of Haldane's group's work in Miller's diary, April 17-22, 1937, RG12.1, RFA.

<sup>915</sup> Grüneberg and Haldane, 1937/1938. Lewis and Hunt, 1984, 243. The work must have continued until about April 1937, when Haldane discussed it with the RF officer, H. M. Miller. (Miller's diary, April 17-22, 1937, RG12.1, RFA).

<sup>916</sup> See Chapter Two (section 2.2.5) for further details.

The genetics work of the DoZ/B became more focused during 1936/1937. During this period the RF encouraged Haldane to form a programme of research focused on one area of genetics. As old projects drew to a close and staff members left, the RFs desire for more focused research may have influenced Haldane's decision not to try to renew them. The area left was population genetics, the highest research priority previously. The choice of population genetics therefore seems to have been made from legacy. That legacy arose partly from Haldane's interests and partly because the work could be done with *Drosophila*, the organism that best met the needs of Haldane's staff.

#### 5.2.1.5 1938/1939

The work of the department changed little during 1938 and 1939. In 1938 Haldane obtained two years worth of funding from the RF to continue the work of the department. The result of the funding was just that.

Population genetics continued in the department as before. In November 1939 the main finding of the *Drosophila* genetics work was reported as being the discovery of over 50% crossing-over in the autosomes of one species.<sup>917</sup> This relates to the work that was being done on the variation found in different natural populations.

The developmental genetics work became more varied but declined in scale. Research continued on the lethal rat gene<sup>918</sup> and was extended to a study of the rats' histology and biochemistry.<sup>919</sup> Also, the development of an inherited cataract was studied in the rat<sup>920</sup> and the development of different types of anaemia was studied in mice.<sup>921</sup> However, the amount of research on this area declined, firstly, when Bedichek returned to America in August 1937<sup>922</sup> and, secondly, at the start of the Second World War. At that time, Haldane got rid of

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<sup>917</sup> Miller's diary, November 6, 1939, f579, b45, s401D, RG1.1, RFA.

<sup>918</sup> Fell and Grüneberg, 1939. Also see correspondence between Fell and Gruneberg, 1937-1939, folder Fang-Firschberg, b5, Grüneberg papers.

<sup>919</sup> Fell and Grüneberg, 1939.

<sup>920</sup> Bourne and Grüneberg, 1939.

<sup>921</sup> Grüneberg, 1939.

<sup>922</sup> Grüneberg to Dunn, 24 August 1937, folder Grüneberg, Hans III, Dunn papers.

most of the mouse stocks<sup>923</sup> and Grüneberg, who had conducted the developmental genetics work, began writing a book.<sup>924</sup> However, some work continued, for example that on anaemia, on the flexed tailed rat and on hearing difficulties in mice.<sup>925</sup>

The human genetics work also continued. At the end of 1939 Haldane reported that he was working on another case of linkage with colour blindness.<sup>926</sup> Haldane's interest in homogeneity also continued. This had previously been expressed through the investigation of variation in wild populations and his work on inbreeding. In 1939 he did some theoretical work on a homogeneity test.<sup>927</sup>

During 1938/1939 the work of the department changed little. This reflected the department's stability in terms of both staff and funding, which was provided by the RF.

#### 5.2.1.6 Problem Choice at the DoZ/B in Conclusion

This section has shown a number of influences on problem choice. Most importantly, there was Haldane's vision of genetics at the DoZ/B, which was based upon his own interests and background. The background, training and position of his staff were also important. Their training determined which sorts of work they could conduct. Only Koller, for example, undertook cytological research. Their generally insecure institutional positions favoured the use of *Drosophila*. This in turn favoured population genetics over physiological genetics, Haldane's two main interests. In 1936/1937 the RF tried to make the department focus on one area of genetics. The variety of research conducted at the DoZ/B decreased considerably at the time. It contracted onto the largest area of research, population genetics because there was little impetus for change.

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<sup>923</sup> Haldane to "Sir", 22 September 1939, f579, b45, s401D, RG1.1, RFA.

<sup>924</sup> Miller's diary, November 6, 1939, f579, b45, s401D, RG1.1, RFA. See also Grüneberg, 1943.

<sup>925</sup> Miller's diary, November 6, 1939, f579, b45, s401D, RG1.1, RFA.

<sup>926</sup> Haldane to Weaver, 3 November 1939, f579, b45, s401D, RG1.1, RFA.

<sup>927</sup> Haldane to Weaver, 3 November 1939, f579, b45, s401D, RG1.1, RFA.

The problems tackled at the DoZ/B were loosely constitutive of genetics. Haldane was happy to reach out to other disciplines such as physiology, evolution studies and cytology to gain research problems. Genetics was therefore treated as an outward looking subject. Very little transmission genetics was conducted at the DoZ/B.

### 5.2.2 Problem Choice at the IAG

Problem choice was far more complicated at the IAG than the DoZ/B. The bodies that funded the Institute had a strong influence over the work conducted. Their influence was far stronger than Crew's, who had a differing vision of genetics at the IAG. However, personal interests were important to problem choice at the IAG. This was seen most clearly following Muller's employment at the Institute. At this time two different visions of genetics co-existed in the Institute, because there were the resources to support both.

#### 5.2.2.1 1930-1932

In 1930 Crew described the work occurring at the IAG as coming under six headings: "Formal Genetics... Physiological Genetics... Sex Biology... Animal Husbandry... Miscellaneous activities... Teaching."<sup>928</sup> In this section I provide examples of what Crew meant by the different headings. I show that the relative extent of research occurring in each of the five areas depended on the funding they received. The areas themselves arose from the Institute's breeding background.

Under the heading 'formal genetics', Crew placed studies conducted on the transmission of characters between generations regardless of the organism used for the research.<sup>929</sup> Such genetics research was done under Crew's direction.<sup>930</sup> Between 1930 and 1932 such work included an investigation of a sex-linked

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<sup>928</sup> A7, folder Memos, financial reports, IAGA. My interest in this Chapter is in research, and therefore I will not discuss teaching. A comparison of teaching at the two institutes would be a legitimate and interesting comparison to make but this lies outside the scope of my dissertation.

<sup>929</sup> A7, folder Memos, financial reports, IAGA.

<sup>930</sup> Memo 4, folder Memos, financial reports, IAGA.

lethal gene in *Drosophila*<sup>931</sup> and a gene that was sometimes dominant and sometimes recessive.<sup>932</sup> It also included cytogenetic studies such as the investigation of the X-chromosome in *Drosophila*,<sup>933</sup> the relationship between chiasmata and crossing-over,<sup>934</sup> and an attempt to explain asymmetrical leg-colour in fowl as an outcome of non-disjunction of the chromosomes.<sup>935</sup> This work was therefore a mixture of transmission genetics, and genetics that reached out to cytology.

Crew defined the work on 'physiological genetics' as research on the causes of mutations and investigations of what genes are and how they act.<sup>936</sup> Such work was also done under Crew's direction<sup>937</sup> and between 1930 and 1932 included studies of the genetic factor for the age of maturity in mice and the genetics of hairlessness in mice.<sup>938</sup>

The third heading Crew grouped the Institute's work under was 'sex biology'. Crew described this work as an analysis of sex and the physiological agencies that controlled it.<sup>939</sup> Between 1930 and 1932 a lot of work was carried out on this subject. In the 1929/1930 Annual Report, such work on the mouse was reported as:

"maturity in the female, mating during pregnancy, lactation interval, puberty and maturity and the effect of density on adult mouse population."<sup>940</sup>

Other sex biology work included research on the physiology of birth,<sup>941</sup> the effect of castration on the secondary sexual characters of fowl,<sup>942</sup> and the effect of light

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<sup>931</sup> Crew and Lamy, 1931/1932.

<sup>932</sup> Crew and Lamy, 1932.

<sup>933</sup> Koller, 1932b.

<sup>934</sup> Crew and Koller, 1932. Bryden, 1932.

<sup>935</sup> Crew, 1931/1932. Crew to Dunn, April 1, 1933, folder Crew, F.A.E., Dunn papers.

<sup>936</sup> A7, folder Memos, financial reports, IAGA.

<sup>937</sup> A8, folder Memos, financial reports, IAGA.

<sup>938</sup> Annual Report, 1929-1930, folder IAG Annual Reports, IAGA. Crew and Mirskaia, 1930. Crew and Mirskaia, 1931/1932.

<sup>939</sup> A7, folder Memos, financial reports, IAGA.

<sup>940</sup> Annual Report, 1929/1930, folder IAG Annual Reports, IAGA.

<sup>941</sup> Memo 4, folder Memos, financial reports, IAGA.

<sup>942</sup> Greenwood and Blyth, 1932.



on the oestrous cycle in sheep.<sup>943</sup> This type of research dominated the work of the IAG because it received the most funding. Sex biology was a typical part of the Institute's breeding research and so was funded by the recurrent grants the location received. Between 1930 and 1932 the research was also supported by funding provided by Macaulay, as discussed in Chapter Three (section 3.3.2.1). In 1930/1931 the section brought in 45% of the location's income from Macaulay alone.

The next heading was 'animal husbandry'. Crew wrote that such work incorporated genetics and physiology into livestock breeding.<sup>944</sup> At the Institute it included:

“collect[ing] information on the mode of inheritance of those characters that in their combination go to make the bacon pig; on the inheritance of fecundity; of early maturity; of seedy cut, etc.”<sup>945</sup>

and:

“collect[ing] information concerning the mode of inheritance of high milk yield and of milk constitution [in goats].”<sup>946</sup>

The final type of research Crew identified occurring at the Institute in 1930 was 'miscellaneous activities'. For this he gave the example of the pregnancy diagnosis station the IAG had set up with the university's Midwifery Department.<sup>947</sup> Other miscellaneous activities included Crew's repetition of McDougall's experiments.<sup>948</sup> McDougall claimed to have found evidence in support of the Lamarckian theory of evolution. Crew spent five years from 1930

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<sup>943</sup> Memo 4, folder Memos, financial reports, IAGA.

<sup>944</sup> A7, folder Memos, financial reports, IAGA.

<sup>945</sup> Memorandum: Application for a Special Grant for Research on Pig and Goat-Breeding, folder Memos, financial reports, IAGA. See also A7, folder Memos, financial reports, IAGA.

<sup>946</sup> Memorandum: Application for a Special Grant for Research on Pig and Goat-Breeding, folder Memos, financial reports, IAGA.

<sup>947</sup> A7, folder Memos, financial reports, IAGA.

<sup>948</sup> Annual Report, 1935/1936, folder IAG Annual Reports, IAGA.

repeating the work which tested how quickly rats learnt to associate light with pain and whether this was inherited.<sup>949</sup>

The five areas of research Crew identified all related to questions of animal breeding. Transmission genetics and cytogenetics investigated the mechanics of inheritance, which was important to breeding higher yield agricultural animals. Physiological genetics investigated how genes act and therefore whether it was possible to produce animals with higher yields by interfering with their physiology. Sex biology studied the process of breeding and how it could be encouraged. Animal husbandry investigated how to apply these findings to agricultural animals. The miscellaneous activities were also related to inheritance and breeding. This relation to animal breeding arose from the Institute's original function as an animal breeding research department. The recurrent funding the Institute received from the ARC meant there had to be a committee to direct and control the location, as discussed in Chapter Three (section 3.2.3.1). This committee ensured the Institute fulfilled its function as a location for animal breeding research. However, between 1930 and 1932 the function was skewed towards sex biology because of external funding.

#### 5.2.2.2 1932-1935

In 1932 the work of the Institute began to change. Both the sex biology and the animal husbandry sections contracted due to the loss of funding.

The most drastic change affected the sex physiology group. Crew later recalled that this section of the department had grown out of proportion prior to the depression.<sup>950</sup> However, by June 1932 the work was beginning to be cut back and notice was given to some of the section's members of staff.<sup>951</sup> In 1934 the head of the sex physiology section was given notice.<sup>952</sup> A year later it was recorded that work on sex physiology had ended.<sup>953</sup> The sex physiology group and their

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<sup>949</sup> Interview with Crew, CD 7, IAGA.

<sup>950</sup> Interview with Crew, CD 7, IAGA.

<sup>951</sup> M12, folder Minutes, IAGA.

<sup>952</sup> M17, folder Minutes, IAGA.

<sup>953</sup> M19, folder Minutes, IAGA.

work were lost from the Institute because the funding they received from Macaulay failed, as discussed in Chapter Three (section 3.3.2.1). The IAG could not afford to support the group without this money.

This is not to say that sex biology research entirely ended in the department. Alan Greenwood's work on sex physiology in fowl continued. However, Greenwood's work was also under threat for a time during this period as the ARC withdrew their support for it.<sup>954</sup> Greenwood and his work survived because he undertook other work as well. From 1933 he tested the effects of various hormones on castrated fowl.<sup>955</sup> This was still sex physiology work, but done as a service task for another scientist rather than as part of Greenwood's own experimental programme.

The animal husbandry section also contracted between 1932 and 1935. In 1932 notice was given to Alexander Calder,<sup>956</sup> who worked on pigs and horses,<sup>957</sup> and I.W. Parnell, who worked on sheep.<sup>958</sup> Both of these redundancies were due to funding withdrawals, the former on the part of the DC,<sup>959</sup> the latter due to an Empire Marketing Board grant expiring.<sup>960</sup> The work of both men continued, however, at least for a time. In 1933 A.D. Buchanan Smith was reported to be working on how the same weight gain could be acquired in pigs while feeding them less food. He also researched the genetics of cattle and horses.<sup>961</sup> Parnell's work on sheep was continued by W.C. Miller until 1935 when he left the department.<sup>962</sup>

Formal genetics, physiological genetics and the department's miscellaneous activities fared much better during this time. In terms of formal genetics Rowena Lamy and F.A.E. Crew worked on the linkage groups of *Drosophila pseudo-*

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<sup>954</sup> Miller's diary, November 17, 1932, RG12.1, RFA.

<sup>955</sup> Miller's diary, April 28, 1933, RG12.1, RFA.

<sup>956</sup> M12, folder Minutes, IAGA.

<sup>957</sup> Deacon, unpublished, p. 20, folder Histories of the Institute, IAGA.

<sup>958</sup> M13, folder Minutes, IAGA.

<sup>959</sup> M12, folder Minutes, IAGA.

<sup>960</sup> M13, folder Minutes, IAGA. M17, folder Minutes, IAGA.

<sup>961</sup> Miller's diary, April 28, 1933, RG12.1, RFA.

<sup>962</sup> M17, folder Minutes, IAGA. Anonymous to Sir Thomas, 10 October 1935, folder IAG Annual Reports, IAGA.

*obscura*<sup>963</sup> and the genetics of budgerigars.<sup>964</sup> Crew also looked at the genetics of mouse coats.<sup>965</sup> In 1932 the ARC commented upon the department's lack of a cytologist.<sup>966</sup> However, Koller, Crew and William Bryden all worked on cytogenetics between 1932 and 1935. However, Bryden's last paper in the *Journal of Genetics* was published in 1933 and there is no evidence of his presence in the department after that time. Koller also left the department at the end of 1934. He wrote to the cytologist, Cyril Darlington:

"I told Crew definitely that I am unable to stay here any longer, knowing that he has no money at all."<sup>967</sup>

At the start of 1932 there had been no cytogeneticist in the department and by the end of 1934 there was none once again. However, in between cytogenetics had commanded a fair amount of interest.

Physiological genetics was studied between 1932 and 1935 at similar levels to 1930-1932. The majority of the work in the previous period had been conducted by Luba Mirskaia. She left the department in 1932 as the Macaulay funding ended.<sup>968</sup> However, Charlotte Auerbach took up physiological genetics in 1933, following her arrival at the Institute to study for a PhD. When Auerbach arrived at Edinburgh she had not studied genetics before. However, she had previously begun postgraduate research on developmental physiology under Otto Mangold in Germany. She therefore chose to study developmental genetics at the IAG. Her PhD was accepted in 1935.<sup>969</sup> It seems that the personal backgrounds of staff were important at the IAG as well as at the DoZ/B.

The miscellaneous activities in the department also continued. The pregnancy diagnosis laboratory came under threat when Berthold Wiesner left the department at the end of 1934, since he had organised the laboratory. However,

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<sup>963</sup> See for example, Crew and Lamy, 1934 and Crew and Lamy, 1935a.

<sup>964</sup> Miller's diary, December 6 and 7, 1935, RG12.1, RFA.

<sup>965</sup> See for example, Crew, 1933.

<sup>966</sup> A8, folder Memos, financial reports, IAGA.

<sup>967</sup> Koller to Darlington, 14 August 1934, folder J.122, box c.110, Darlington papers.

<sup>968</sup> M12, folder Minutes, IAGA states that Mirskaia had been given notice and she is not listed as a member of staff in the minutes from M13, folder Minutes, IAGA.

<sup>969</sup> Beale, 1995, 25.

by the end of 1935 it had expanded<sup>970</sup> and was financially independent, making its future seem secure.<sup>971</sup> Crew's repetition of McDougall's work also continued until 1935/1936 when he published the results.<sup>972</sup>

The amount of research conducted in each of the five areas between 1932 and 1935 was therefore dependent upon the funding received. It was also dependent upon the training of staff, as seen in the case of Auerbach.

### 5.2.2.3 1935-1937

1935 marked another inspection of the Institute by the ARC. The Council agreed to fund a reduced department consisting of a geneticist, cytologist, physiologist, agricultural geneticist and a statistician.<sup>973</sup> In this section I show how this resulted in the decrease of the location's research in general, but in the growth of some areas.

Formal genetics profited from the ARC's agreement that the location should have a cytologist as a permanent member of staff. At the end of March 1935 Koller returned to the Institute as their cytologist.<sup>974</sup> He portrayed the Institute as being a different place since the changes, writing:

“The Institute is in a turmoil, nobody knows, [sic] what one must do or expected to do. I myself feel, that I am a lost man here. Empty rooms, desks, shelves and I must organise the work.”<sup>975</sup>

However, the section lost out from Hugh Donald's move to animal husbandry. Donald worked on *Drosophila* genetics between 1934 and 1936 for his thesis, before becoming a junior lecturer in animal husbandry at the Institute.<sup>976</sup>

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<sup>970</sup> Anonymous to Sir Thomas, 10 October 1935, folder IAG Annual Reports, IAGA. Interview with Crew, CD 3, IAGA.

<sup>971</sup> Miller's diary, December 6 and 7, 1935, RG12.1, RFA.

<sup>972</sup> Annual Report, 1935-1936, folder IAG Annual Reports, IAGA.

<sup>973</sup> Weaver's diary, May 11, 1935, RG12.1, RFA.

<sup>974</sup> Koller to Darlington, 29 March 1935, folder J.123, box c.110, Darlington papers. Miller's diary, March 13, 1935, RG12.1, RFA.

<sup>975</sup> Koller to Darlington, 29 March 1935, folder J.123, box c.110, Darlington papers.

<sup>976</sup> [http://www.nahste.ac.uk/isaar/GB\\_0237\\_NAHSTE\\_P0776.html](http://www.nahste.ac.uk/isaar/GB_0237_NAHSTE_P0776.html), accessed 14 August 2003. Annual Report, 1935-1936, folder IAG Annual Reports, IAGA.

Work on animal husbandry increased slightly during this period. At the end of 1935 there was nobody working under Buchanan Smith.<sup>977</sup> In 1936, as mentioned above, Donald was employed as his assistant. Pickard's work on rabbits, begun at the end of the 1920s, also continued throughout the period.<sup>978</sup> This growth appears to have been due to the excessive losses the section underwent prior to 1935, which left them short-staffed.

Sex biology retained the size it had attained after the entire sex physiology group left. Greenwood continued his work on the subject<sup>979</sup> and was joined by A.M. Hain and J.S. Wu. Hain worked as a visitor in the department<sup>980</sup> on problems such as the effect of sex hormones on mice and rats<sup>981</sup> and Wu investigated testis size in *Drosophila*.<sup>982</sup>

Physiological genetics was studied slightly less in the mid-late 1930s. Auerbach concentrated on transmission genetics once she had submitted her PhD in 1935.<sup>983</sup> However, gene action remained a concern of the Institute. Flora Cochrane, for example, studied the development of eye colour in *Drosophila*.<sup>984</sup>

The Institute's miscellaneous activities also reduced in size during the period. Crew's repetition of McDougall's Lamarckian experiments finally ended in 1935/1936.<sup>985</sup> The pregnancy diagnosis laboratory appears to have continued to be run throughout the period.<sup>986</sup>

The research conducted between 1935 and 1937 was therefore very dependent upon the action of the ARC in 1935. At the same time Crew was determined to

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<sup>977</sup> Anonymous to Sir Thomas, 10 October 1935, folder IAG Annual Reports, IAGA.

<sup>978</sup> M21, folder Minutes, IAGA.

<sup>979</sup> M19, folder Minutes, IAGA.

<sup>980</sup> Annual Report, 1935-1936, folder IAG Annual Reports, IAGA.

<sup>981</sup> Hain and Robson, 1936.

<sup>982</sup> Wu, 1937/1938.

<sup>983</sup> Beale, 1995, 26.

<sup>984</sup> Cochrane, 1936.

<sup>985</sup> Annual Report, 1935-1936, folder IAG Annual Reports, IAGA.

<sup>986</sup> Miller's diary, December 6-7, 1935, RG12.1, RFA.

focus the IAG onto cytogenetic research.<sup>987</sup> This, however, does not appear to have had a major impact of the work of the Institute.

#### 5.2.2.4 1938-1939

In November 1937 H.J. Muller joined the IAG.<sup>988</sup> In this section I show that, while the rest of the Institute's research continued as before, Muller quickly changed the balance of research at the Institute.

Between the end of 1937 and the start of 1940 Muller led a programme of research into the process by which gross structural changes were caused in chromosomes by radiation. Muller conducted this research in collaboration with ten other researchers at the IAG.<sup>989</sup> The amount of research on formal genetics at the Institute therefore increased significantly during this period. The areas of formal genetics previously worked on were also continued. Koller continued to research cytogenetic problems such as the relationship between coiling and chiasmata during meiosis.<sup>990</sup> Crew and Lamy investigated problems such as mosaicism in *Drosophila*<sup>991</sup> and Crew and Auerbach studied problems such as the genetics of a coat character in mice.<sup>992</sup>

The other area of research that increased slightly in size was animal husbandry. Buchanan Smith, Pickard and Donald continued their research in this area. They were joined by Galpin, who researched the growth rate of chickens, because a special grant was obtained for this research.<sup>993</sup>

Sex biology retained its size. Greenwood continued his research in this area,<sup>994</sup> working with Janet Blyth on sexual plumage in fowl.<sup>995</sup> He was also joined by

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<sup>987</sup> Anonymous to Sir Thomas, 10 October 1935, folder IAG Annual Reports, IAGA.

<sup>988</sup> Crew to Sir, 17 February 1938, f44, b4, s405D, RG1.1, RFA.

<sup>989</sup> Muller, 1940, 59.

<sup>990</sup> Annual Report, 1938-1939, folder IAG Annual Reports, IAGA.

<sup>991</sup> Crew and Lamy, 1938/1939.

<sup>992</sup> Crew and Auerbach, 1939.

<sup>993</sup> M23, folder Minutes, IAGA.

<sup>994</sup> M23, folder Minutes, IAGA.

<sup>995</sup> Greenwood and Blyth, 1938a and Greenwood and Blyth, 1938b.

Hugo Merton, who researched reproduction in mice.<sup>996</sup> Physiological genetics was still researched at the Institute, though not to a great extent. Cochrane, for example, continued her studies of the development of eye colour in *Drosophila*.<sup>997</sup> The pregnancy diagnosis laboratory also continued, so that some miscellaneous activities were also retained.

The arrival of Muller precipitated the study of a new research project in 1938 and 1939; chromosomal change. This became one of the IAG's major research projects during the period. Crew wanted to change the direction of the Institute towards cytogenetics in 1935. Prior to 1937 he had failed. From November 1937 he succeeded through Muller. Muller succeeded in part because he inspired postgraduate students to work with him and in part because he obtained funding from the Scottish Cancer Control Organisation.<sup>998</sup>

#### **5.2.2.5 Problem Choice at the IAG in Conclusion**

This section demonstrates that problem choice at the IAG was under far greater institutional control than at the DoZ/B. The ARC's funding of the department led to a committee being appointed to direct and control the IAG.<sup>999</sup> This committee ensured that the problems tackled contributed to the field of animal breeding. External funding still influenced the extent to which different areas were researched. For example, the extent to which sex biology was researched during the decade was highly dependent upon Macaulay's funding of it. The training of researchers was also important, as seen in Auerbach's case. However, Crew had far less control over the research conducted at the IAG than Haldane at the DoZ/B. This is seen from the lack of success Crew had in changing the Institute's direction from 1935 to 1937. Muller succeeded to some extent where Crew failed. Muller appears to have inspired more confidence in postgraduate students, whose labour came cheaply, and in funding bodies, whose backing was necessary for any new programme of research.

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<sup>996</sup> See for example, Merton, 1938. Annual Report, 1938-1939, folder IAG Annual Reports, IAGA.

<sup>997</sup> Cochrane, 1938.

<sup>998</sup> Memorandum, December 12, 1938, f44, b4, s405D, RG1.1, RFA.

<sup>999</sup> Crew to Mann, 25 May 1926, f570, b40, s2, IEBA.



Problem choice was quite different at the IAG and the DoZ/B. At the DoZ/B, genetics was synthesised with other disciplines. At the IAG, formal genetics and physiology were studied in the same location for the same purpose; breeding. However, the approaches and ideas of the two were not synthesised to tackle individual problems. The only synthesis that took place was between genetics and cytology.

### **5.2.3 Problem Choice at the DoZ/B and the IAG in Conclusion**

Problem choices at the DoZ/B and the IAG were very different. The DoZ/B saw genetics as an outward looking discipline that could be fused with other disciplines such as evolution studies and physiology. Ideas and methods from these different disciplines were used to tackle the same research problem. The IAG saw genetics as a more tightly bound discipline. The ideas and methodologies from various disciplines, including genetics, were used alongside each other to investigate breeding. However, the ideas and methods of different disciplines were not used to tackle the same individual problem, with the sole exception of cytogenetics.

The locations also varied with regard to the influences upon their choices of problem. The IAG was subject to strong controls upon the type of research conducted from the Animal Breeding Committee, which was necessitated by the funding it received from the ARC. The ARC itself also strongly influenced the extent of research conducted in different areas. This contrasts greatly with the DoZ/B where the major influence was Haldane's personal interests. However, lack of funding forced other constraints on Haldane. He required work to be done with an inexpensive organism with a fast reproductive turn-over because his staff were either PhD students or in unstable positions. This favoured *Drosophila* work, and thus population studies.

## 5.3 Problem Choice at Other Locations

In this section I investigate the problems tackled at other British genetics locations during the 1930s. This demonstrates that the differences seen between the DoZ/B and the IAG were typical of the differences between their respective settings.

### 5.3.1 Problem Choice in the Academic Setting

In this section I show that the main areas of research in the academic setting were transmission genetics, evolutionary genetics and cytogenetics. Transmission genetics was studied mainly in genetics departments, evolutionary genetics tended to be studied in zoology departments, and cytogenetics in botany departments. A minor amount of physiological genetics was also conducted. Genetic locations tended to focus on one area of research.

One type of genetics problem tackled in the academic setting was transmission genetics. This was conducted by Punnett at the Genetics Department at Cambridge University and by Ruth Bamber and Catherine Herdman at Liverpool University. Punnett's work was directed towards understanding the mechanism of heredity, mainly through linkage studies of fowl.<sup>1000</sup> Bamber and Herdman's work investigated the progeny of one male cat and worked out its gametes.<sup>1001</sup> Bamber also investigated the link between white coat, blue eyes and deafness in cats.<sup>1002</sup>

Evolutionary genetics was studied at Aberdeen University, as well as at the DoZ/B. At Aberdeen, Cecil Gordon worked on the genetic dynamics of populations of a polymorphic isopod<sup>1003</sup> and the population genetics of *Drosophila* and rabbits.<sup>1004</sup>

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<sup>1000</sup> Crew, 1967, 318, 325-326.

<sup>1001</sup> Bamber and Herdman, 1932.

<sup>1002</sup> Bamber, 1933.

<sup>1003</sup> Miller's diary, November 18 and 19, 1938, RG12.1, RFA.

<sup>1004</sup> Tisdale's diary, June 27-28, 1937, f39, b3, s405D, RG1.1, RFA.

Cytogenetics was the focus of research at the Botanical Laboratory, King's College, London. Studies included the investigation of chromosome rings,<sup>1005</sup> chiasmata, crossing-over and mutation<sup>1006</sup> and the study of non-disjunction.<sup>1007</sup> Cytogenetic studies were also performed at the botany department in Manchester. F.W. Sansome investigated sex determination,<sup>1008</sup> and E.R. Sansome the cytology of *Pisum* hybrids.<sup>1009</sup>

### 5.3.2 Problem Choice in the Breeding Setting

This section shows that the type of problems tackled in the breeding setting were directed towards gaining a better understanding of the breeding of particular organisms rather than the process of breeding in general. This was also a finding of Chapter Four (see section 4.3.2-4.3.3). However, not all the characters studied were of immediate benefit to agriculture or horticulture. The research conducted was a mixture of transmission genetics, cytology and cytogenetics. Genetics tended to be studied alongside other disciplines at breeding locations, rather than being synthesised with them.

Transmission genetics research was conducted at Kew Gardens. For example, breeding experiments were conducted with *Saxifraga*<sup>1010</sup> and variation studied in *Anthyllis*.<sup>1011</sup> Sex in *Ranunculus*<sup>1012</sup> was also studied. All this research was of benefit to horticulture because the ability to breed plants and control variation was vital to horticulturalists.

Transmission genetics research was also conducted at the Scottish Plant Breeding Station. Investigations included the inheritance of grain colour in oats,<sup>1013</sup> tuber colour in potatoes<sup>1014</sup> and resistance to Wart disease in potatoes.<sup>1015</sup> The latter

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<sup>1005</sup> Catcheside, 1933.

<sup>1006</sup> Sweet, 1937/1938.

<sup>1007</sup> Ford (C.E.), 1936.

<sup>1008</sup> Sansome (F.W.), 1937/1938.

<sup>1009</sup> Sansome (E.R.), 1938.

<sup>1010</sup> Marsden-Jones and Turrill, 1934.

<sup>1011</sup> Marsden-Jones and Turrill, 1933.

<sup>1012</sup> Marsden-Jones and Turrill, 1935.

<sup>1013</sup> Robb, 1932.

<sup>1014</sup> Black, 1933.

was an important agricultural factor, but the previous two characters were not. The latter was thus immediately relevant to agriculture, while the former two helped the Station to understand inheritance in agriculturally important crops.

Transmission genetics was also studied at the Welsh Plant Breeding Station. For example, they researched the genetics of flower colour in red clover<sup>1016</sup> and the genetics of cyanogenesis in white clover.<sup>1017</sup> The Station also researched cytology. For example, they researched the cytology of intergeneric hybrids.<sup>1018</sup> Hybrids of herbage grasses were the focus of much of the station's genetics and cytological research. For example Jenkin studied the difference between intergeneric and interspecific crosses<sup>1019</sup> and Ellison studied the cytological causes of sterility in a hybrid.<sup>1020</sup> This research was again a mixture of pure research and research of more direct applicability to agriculture. The Station directed its research towards the improvement of grasslands in general.<sup>1021</sup> Knowledge of sterility and the results of hybridisation would be useful to breeding herbage grasses. The genetics of flower colour in clover was not of obvious immediate benefit.

Most of the genetics research at the School of Agriculture at Cambridge were cytogenetic studies of hybrids. For example, they studied a cross between a triploid radish and a turnip,<sup>1022</sup> the fertility of *Raphanus sativus* / *Brassica oleracea* hybrids<sup>1023</sup> and the cytogenetics of *Triticum sphaerococcum* when crossed with *Triticum vulgare*.<sup>1024</sup> Such research was of immediate applicability to agriculture.

Most of the research conducted at the JI was either genetic or cytological. For example genetics research included Haldane and D. de Winton's study of the

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<sup>1015</sup> Black, 1935.

<sup>1016</sup> Williams, 1935.

<sup>1017</sup> Williams, 1939.

<sup>1018</sup> Peto, 1933/1934.

<sup>1019</sup> Jenkin, 1933/1934.

<sup>1020</sup> Ellison, 1936.

<sup>1021</sup> Palladino, 2002, 51.

<sup>1022</sup> Morris and Richharia, 1937.

<sup>1023</sup> Howard, 1938.

<sup>1024</sup> Ellerton, 1939.

genetics of diploid *Priumula*,<sup>1025</sup> and Eileen Sutton's investigation of the genetics of *Tropaeolum*.<sup>1026</sup> Cytological research included James Philp's investigation of the cytology of *Saxifraga* species and hybrids<sup>1027</sup> and Margaret Upcott's study of the cytology of *Lycopersicum*.<sup>1028</sup> The research often focused on hybrids and problems of fertility.<sup>1029</sup>

Research at the JI also included studies that drew on both genetics and other disciplines. For example, Mather and Darlington studied the relationship between crossing-over and chiasmata, a cytogenetic problem.<sup>1030</sup> W.J.C. Lawrence and Rose Scott-Moncrieff studied biochemical genetics,<sup>1031</sup> and F.G. Brieger studied developmental genetics.<sup>1032</sup>

### **5.3.3 A Comparison of Genetics and Cytological Research across the Settings**

The main areas of overlap across the settings were in transmission genetics and cytogenetics. In this section I compare two pieces of research that were done in the breeding and academic settings. Both studied firstly the transmission of characters across generations and secondly the cytology that underlay the results gained. I show in this section that research in the breeding setting was far more empirically based than in the academic setting, which tended to be theoretically based.

#### **5.3.3.1 Experiments with *Oenothera* in the Academic Setting**

In 1932 the King's College cytogeneticists, R.R. Gates and D.G. Catcheside, published the results of breeding experiments they had performed with *Oenothera*.<sup>1033</sup> The pair were trying to establish what constituted a new species

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<sup>1025</sup> De Winton and Haldane, 1933.

<sup>1026</sup> Sutton, 1939.

<sup>1027</sup> Philp, 1934.

<sup>1028</sup> Upcott, 1935.

<sup>1029</sup> See, for example, Brieger, 1935, Tseng, 1938 and Upcott and Philp, 1939.

<sup>1030</sup> Mather, 1933 and Koller and Darlington, 1934.

<sup>1031</sup> Lawrence and Scott-Moncrieff, 1935 and Scott-Moncrieff, 1936.

<sup>1032</sup> Brieger, 1937.

<sup>1033</sup> Gates and Catcheside, 1932.

in the *Oenothera* genus. When two species were crossed, two hybrid forms were often produced that bred true. These results had been explained as due to two haploid complexes, each of which may be involved in the cross, although one form was often unviable in either the pollen or eggs. The complexes were composed of completely linked chromosomes, often in chains or rings. The composition of the complexes in some species had previously been identified and the relationships between them established. Gates and Catcheside tried to do the same for some *Oenothera* species that had not previously been analysed. This involved performing crosses and describing the phenotypes, so the inheritance of different complexes could be established. Findings with regards to the hetero- or homo-zygosity of the species (whether they had two identical complexes or two different ones) were confirmed by studies of the development of seeds. These were expected to fail more when the gametes were similar and the complexes different. The viability of different complexes in pollen was also studied. Using their data and the cytological data that was available the pair suggested how the species were cytologically related to each other.

The cytology of the hybrids formed during the experiments was also studied by Catcheside.<sup>1034</sup> The main purpose of the research was to establish the number of chromosomes and their formation in each of the hybrid forms. However, Catcheside also studied the number of chiasmata to form in each chromosome arrangement. This revealed that chiasmata occurred far less often in rings than pairs, implying that pairing did not occur along the whole chromosome length. Crossing-over occurred at a frequency of over fifty percent at the chromosome ends and not at all in the middle of the chromosomes. This helped to explain the ring formation. The rings appeared to break at random, hence chains of chromosomes of various different lengths were observed. Interference to crossing-over was also established and identified as a possible key to understanding the different chromosome arrangements seen.

Gates and Catcheside's research was theoretically driven. The work was intended to reveal how species of *Oenothera* differed from each other and thus add to the

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<sup>1034</sup> Catcheside, 1933.

understanding of how species can form. Catcheside's cytological work was intended to add cytological evidence to the genetical evidence gathered. It also provided information about the mechanics by which the complexes that underlay species were created and destroyed.

### 5.3.3.2 Experiments with *Saxifraga* in the Breeding Setting

The phenomena studied with *Saxifraga* in the breeding setting was very similar to that studied in the academic setting, but the papers published on the phenomena differed greatly. The Kew geneticists E.M. Marsden-Jones and W.B. Turrill crossed two species of *Saxifraga* and noticed that the F<sub>1</sub> generation appeared to breed true. The F<sub>2</sub> and F<sub>3</sub> were designated a new species. In the genetics paper Marsden-Jones and Turrill published in 1934 they described the back-crosses they performed with the F<sub>1</sub>-F<sub>3</sub> generations, the phenotypes obtained and the degree of uniformity seen. The pair concluded that genic segregation was seen but generally polyploidy prevented segregation from occurring. The paper differed from Gates and Catcheside's because the pair did not link their results to the wider problem of species formation and constitution. Their results, while having wider implications, were not portrayed as such.

The plants were passed to the John Innes cytologist, J. Philp, who studied the cytological basis for the genetical results.<sup>1035</sup> Philp counted the number of chromosomes in plants of the two original species and in plants from the F<sub>1</sub> to F<sub>3</sub> generations. Philp concluded that both original species were allopolyploids (fertile interspecific hybrids). He claimed that this explained why the F<sub>1</sub> was fertile and the F<sub>2</sub> and F<sub>3</sub> differed little from it morphologically. Philp therefore provided the cytological basis for the genetical results. Unlike Catcheside, however, he did not attempt to understand how the chromosome arrangements had arisen.

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<sup>1035</sup> Philp, 1934.

### 5.3.4 Types of Research in Conclusion

There was a large overlap between the research areas studied in the two settings. However, there were also patterned differences, which suggest that setting had some affect on problem choice. The main difference was the study of evolutionary genetics in academic zoology departments. The research area studied at any particular location is best explained with reference to the more specific purpose of the location.

The majority of the research in the breeding setting was transmission genetics, cytology or cytogenetics. Some research was also done on physiological/biochemical genetics. The majority of the research in the academic setting was evolutionary genetics, cytogenetics or transmission genetics. The main difference between the settings was therefore the study of evolutionary genetics in the academic setting and the strong focus on transmission genetics in the breeding setting. This can be explained by the settings concept.

The creation of variation and controlling it was important to the breeding setting. New, beneficial, characters were created by promoting variation. These characters then had to be fixed into the line and variation of that character, minimised. Knowledge of this could be gained from both cytogenetics and transmission genetics, as seen in section 5.3.3.2 above. Variation in plants could be created by hybridisation. Most of the studies in the breeding setting, as noted above, were of hybrids. Understanding how this variation was inherited in the next generations involved transmission genetics studies. Understanding why the variation arose in the first place, and hence how to create or prevent it in future involved cytogenetical studies. The latter were also important to the breeding setting because they helped to explain sterility.

The purpose of the academic setting was not to be able to control variation but to understand inheritance in general. All areas of genetics were therefore legitimately within the academic setting's domain. The areas that were most studied are therefore best explained by considering the more specific purpose of each location. Botany departments aimed to understand plants, especially in



contradistinction to animals. The inheritance of chromosomes appeared to be far more important to explaining the inheritance of characters in plants than in animals. Chromosomal genetics was therefore concentrated in botany departments in the academic setting.

Zoology departments aimed to understand animals. The mechanism of their inheritance was far less controversial during the 1930s than that of plants. Transmission and cytogenetics did not therefore form a major part of genetics research in these departments. Instead genetics was applied to wider problems. Two of the main problems facing genetics were the relationship between evolution and genetics and that between embryology and genetics. In Britain the problem of the relationship between evolution and genetics was quite pressing. Prior to 1910 Mendelian genetics had been resisted by the Biometrians in Britain because it appeared to contradict Darwinian evolution. The work of R.A. Fisher and J.B.S. Haldane had shown that the two were theoretically compatible but no work had been done to confirm that their theories applied to nature. Evolutionary genetics therefore dominated the work of zoology departments.

Some physiological genetics was studied in both settings. This was of relevance to the breeding setting. As pointed out in section 5.2.2.1 above, information about the action of genes may have enabled breeders to modify the organism's physiology rather than/as well as their genetics. As the whole of genetics was within the academic domain, minority areas such as physiological genetics would be expected to be seen as well as the major areas discussed above.

Choice of research area was therefore not solely determined by setting, but by this in conjunction with the more specific purpose of the location, the history of genetics in Britain and the history of genetics more generally. Other explanations for research area can be given. Most of the cytogenetical research done in Britain was conducted with plants. This was part of the explanation given above. However, it could be argued that cytogenetics was performed far more in the breeding setting than the academic because plants were the dominant research organism used there. To understand evolution, variation must be understood. Thus, these studies had evolutionary significance. While this is true, it only

serves to push the burden of explanation further back. Why did the breeding setting and botany departments tend to use plants for research? The answer is because of their purpose. In the latter case, this purpose was to research plants and in the former case it was to research organisms that were agriculturally important in Britain; these tended to be plants.

This highlights another difference between problem choice in the two settings. In the breeding setting it generally involved a choice of both research topic and organism. The Scottish Plant Breeding Station investigated the genetics of potatoes; the Welsh Plant Breeding Station investigated the genetics and cytology of grass. The desired information was about the genetics (or cytology) of a particular organism. This contrasts with the academic setting where problem choice was the same as research topic choice. At Cambridge transmission genetics was studied, at Oxford and Aberdeen population genetics, and at Manchester cytogenetics was studied. The particular organism in which these areas were researched was not the principal concern.

## **5.4 Chromosomal Studies**

One of the main areas of overlap between the research areas studied in the breeding and academic settings was cytogenetics. This area was briefly compared between the settings for two plant genetic locations in section 5.3.3. In this section I investigate the extent to which research topics, within the area of chromosomal research, overlapped between two animal genetic locations in the different settings (the DoZ/B and the IAG). There were three topic areas for chromosomal research: genetic topics, cytogenetic topics and cytological topics. Genetic topics were those that focused their investigation on genes. Cytological topics focused on chromosome structure and/or behaviour and cytogenetic topics investigated both genes and chromosome structure/behaviour. I show that only the IAG researched cytological topics and the extent of its research into cytogenetics far exceeded that done at the DoZ/B. This confirms the findings above, that cytogenetics was far more studied in the breeding setting than in academic zoology departments. I also investigate the methodology that was used

at the IAG and the DoZ/B. I show that cytological methodology was more commonly used at the IAG than the DoZ/B. However, while genetic and cytological methodologies were both commonly used to approach the same problem at UCL, this was not the case at the IAG.

### 5.4.1 Genetics Topics

In section 5.4.1, I investigate the specific genetic topics studied at the DoZ/B and the IAG in the area of chromosomal research, and the methodology used.

#### 5.4.1.1 Inversions

The investigation of chromosomal inversions was not an intrinsically genetic or cytological topic. They could be considered as either an inversion of the gene sequence or an inversion of the chromosome structure. If considered in the first way, the topic became genetic; if in the latter, the topic was cytological. These two ways of viewing inversions also promoted the use of different methodologies. The first way of viewing inversions was necessary to investigate it genetically, the latter to investigate it with cytological methodology.

In this section I show that at both the DoZ/B and the IAG the inversions studied were inferred from anomalous genetics results. They therefore had a genetic understanding embedded into them by their means of discovery. Having become genetic, the primary methodology used to research them was genetic. However, at the DoZ/B, cytological methodology was also used. For this, the cytological understanding of inversions had to be applied; the research topic then became cytogenetic.

While undertaking X-ray experiments Grüneberg discovered a sex linked gene for rough eye surface in *Drosophila melanogaster*.<sup>1036</sup> Grüneberg mapped the gene by creating stocks that contained the rough eye surface allele along with

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<sup>1036</sup> Grüneberg, 1935b, 163. The X-ray experiments probably investigated the frequency lethal genes were produced by X-rays. (Summary of Work in Progress, 3 October 1934, f578, b45, s401D, RG1.1, RFA).

recessive alleles whose loci on the X chromosome were known. He then determined the frequency of crossing-over, as described above, to see how far the gene was from the other genes of known loci. Whilst carrying out this genetics research with genetics methodology, Grüneberg gained three unexpected results. Firstly, cross-over frequencies between the marker alleles were lower than their standard values. Secondly, most of the cross-overs were double. When alleles whose loci were known to be at the far ends of the chromosome were introduced in repulsion, they were left on different chromosomes when crossing over occurred. Finally, the relative cross-over frequencies between different genes were not those expected. For example, less crossing-over was expected between the alleles for yellow and miniature wings than those for yellow and forked bristles. In Grüneberg's stocks more crossing-over occurred between yellow and miniature wings than yellow and forked bristles. The relative positions of the genes on the chromosome therefore seemed to have changed.<sup>1037</sup>

Grüneberg explained the results by postulating an inversion in the X chromosome. As stated above, the inversion was not intrinsically genetic or cytological. However, it was postulated to explain genetic results. It therefore had to have the genetic meaning of a change in gene sequence. This change in gene sequence explained the change in relative crossing-over frequencies between genes. It was also consistent with a reduction in crossing-over frequency. To explain the lack of single crossing-over, the inversion also had to be understood in cytological terms. Grüneberg argued that single crossing-over in an organism with one normal and one inverted X chromosome, which occurred within the inversion, would lead to a pair of chromosomes where one partner had two spindle fibres and the other had none. These would not be viable and thus the postulate of an inversion explained why most of the cross-overs were double.<sup>1038</sup> The spindle fibres were a structural element of the chromosomes. By referring to changes that had occurred to them, Grüneberg was referring to structural changes to the chromosomes, in other words cytological changes.

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<sup>1037</sup> Grüneberg, 1935b, 163-164.

<sup>1038</sup> Grüneberg, 1935b, 164-165.

Grüneberg then tried to locate the inversion. He argued that yellow was outside the inversion and the rest of the characters he was studying were inside it. This was because yellow was the furthest left on the chromosome and all the single cross-overs occurred between yellow and the other characters. As discussed above single crossing-over could not occur inside the inversion, so yellow must be outside it. Grüneberg further argued that to pair during meiosis the chromosomes would have to form a loop. The distance furthest away from a gene outside the inversion would therefore be exactly in the middle of the inversion. The amount of double crossing-over to occur between genes outside the inversion (such as yellow) and the genes in the inversion would therefore increase towards the middle of the inversion and reduce symmetrically away from the middle of the inversion. Grüneberg then argued that due to this symmetry, the frequency of double cross-overs between yellow and the other characters would be limited by either the distance from yellow to the character or the character and the right break of the inversion, whichever was shorter. The right break must therefore be at least the double cross-over length between yellow and cross-veinless beyond cross-veinless, and similarly for all the other characters.

Inversions are not intrinsically cytological or genetic. Grüneberg applied a genetic understanding to it to enable him to use it to explain anomalous genetics results. This, in turn, enabled him to use genetic methodology to investigate it. However, Grüneberg also applied a cytological understanding of the inversion to allow him to draw on cytological theory about pairing in an inversion and thus work out the relative crossing-over values expected at different parts of the inversion.

Since the inversion was recognised as a cytological as well as a genetic phenomenon, it was possible to study it with cytological methodology as well as with Grüneberg's genetic methodology. Koller observed the X-chromosome in the salivary glands of *Drosophila melanogaster* under a microscope.<sup>1039</sup> The observation of slides under a microscope was a methodology commonly used in

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<sup>1039</sup> Koller, 1935b.

cytology. Koller observed a loop configuration during pairing, as Grüneberg had postulated. He noted where it began and ended on the chromosome. By using Painter's chart, which correlated the chromosome appearance with the position of genes on it,<sup>1040</sup> Koller converted his findings of where the inversion ends were in relation to the bands of the chromosome to information about where the ends were in relation to the genes on the chromosome.

Similar work was also conducted at the IAG. The work Crew and Lamy performed to map 'plexus' produced evidence of an inversion.<sup>1041</sup> As Grüneberg found for his inversion, Crew and Lamy found that there was no single-crossing over between two of the alleles and crossing-over was much reduced generally. Crew and Lamy also tried to locate the inversion breaks. From the cross-over classes that occurred, they argued that yellow must be outside the inversion and vermilion and singed inside it. This was because single crossing-over occurred between yellow and vermilion, but not between vermilion and singed. This single crossing-over had to occur at a point between yellow and the start of the inversion, as single crossing-over within the inversion would lead to unviable offspring. The frequency of this single crossing-over therefore also gave some estimate of the distance between yellow and the left break of the inversion. The crossing-over frequencies also indicated that double crossing-over inside the inversion happened most frequently near vermilion. Crew and Lamy argued that since pairing in an inversion began at the middle of the inversion, interference to crossing-over was lowest here. They argued that this implied the centre of the inversion was near to vermilion.

The genetic methodology of Grüneberg and Crew and Lamy did not differ much. Grüneberg argued from the symmetry of crossing-over in the inversion to locate the right break, whereas Crew and Lamy argued that the point of lowest interference to crossing-over must be in the centre of the inversion. The major difference was that Grüneberg drew on cytological methodology to study the inversion as well as genetical. Crew and Lamy did not do so. This is curious. Very little cytological methodology was used in the DoZ/B, as discussed below.

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<sup>1040</sup> See Painter, 1933.

<sup>1041</sup> Crew and Lamy, 1936.

A lot of cytological methodology was used at the IAG, yet Crew and Lamy did not draw upon it. As discussed later in this section, different methodologies were not used to tackle the same problem at the IAG. This suggests that geneticists, cytologists and physiologists worked in isolation from each other.

#### 5.4.1.2 Reversion

The use of both genetic and cytological methodology for studying phenomena that was not intrinsically genetic or cytological at the DoZ/B was also demonstrated when the rough eye surface disappeared from the *Drosophila* stock at the DoZ/B. No similar research on a re-inversion was conducted at the IAG.

Grüneberg<sup>1042</sup> demonstrated that a re-inversion had occurred in the stock using genetic methodology. By means of breeding and examining the phenotypes of the resulting offspring, he showed that the standard cross-over frequencies were seen between marker genes.

Grüneberg argued that the re-inversion was complete because first, the cross-over values were standard and second, non-complete re-inversion would leave active material in the inactive region of the chromosome and/or inactive material in the active region. Single crossing-over would therefore cause either duplication or deficiency of genes. Deficiency would be lethal in males, but this was not observed from breeding crosses. Grüneberg therefore used genetic methodology, and on the basis of the phenotypes observed and genetic theory, argued that a complete re-inversion had occurred. He also pointed out that if the re-inversion was not complete, a loop would be cytologically observable during pairing. This, however, had not been seen by C.W. Emmens, whose work is described below. While Grüneberg only used genetic methodology and theory he pointed towards cytological methodology and theory to support his argument.

Cytological methodology was also used to study the re-inversion at the DoZ/B. C.W. Emmens observed the re-inverted chromosomes using a microscope. This

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<sup>1042</sup> Grüneberg, 1937.

revealed no loop formation, as would be expected according to cytological theory if there was an inversion. Normal banding was also observed compared to Bridges 1935 maps.<sup>1043</sup> Emmens compared the banding he observed using cytological methodology with normal banding. This established that no inversion existed.

#### 5.4.1.3 Homologies

Just as the investigation of inversions was not intrinsically a genetic topic, the study of chromosome homology in different species was not intrinsically genetic or cytological. In this section I describe how it was made a genetic topic at the IAG and the DoZ/B to enable genetic methodology to be used for its investigation.

In 1935 Crew and Rowena Lamy published a paper on the linkage groups in *Drosophila pseudo-obscura*.<sup>1044</sup> Their aim was to map various mutations on the chromosomes of *Drosophila pseudo-obscura* to see what homologies could be identified between its chromosomes and those of *Drosophila melanogaster*.

The methodology used was genetic. Crew and Lamy used breeding techniques to identify the linkage groups of various mutations and to calculate the cross-over frequency between them and marker genes. This methodology allowed them to map the mutations.<sup>1045</sup> Crew and Lamy compared their linkage maps for *Drosophila pseudo-obscura* with those for *Drosophila melanogaster* in the literature. Having identified which parts of the different chromosomes they thought were homologous, the pair argued that their suggestions were backed up by cytological observations. These showed the relative lengths of the chromosomes conformed to their suggestions. The differences in linkage values between some alleles were explained by inversions.

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<sup>1043</sup> Emmens, 1937. Also see Bridges, 1935.

<sup>1044</sup> Crew and Lamy, 1935a.

<sup>1045</sup> Crew and Lamy, 1935a, 15-23.



Christie performed similar research at the DoZ/B. He used X-rays to promote mutations in *Drosophila subobscura*. In his paper,<sup>1046</sup> Christie describes the mutations that arose and gave the ratios for its appearance in the F<sub>1</sub>. The cross-over frequencies between the genes were obtained and used to map the genes on the X chromosome. He then compared the map to that of *Drosophila melanogaster*.

Christie's work differed from Crew and Lamy's in as much that he used X-rays to promote mutations. Crew and Lamy do not state that they did so in their paper. This difference gave Christie's work a slightly different aim. While he investigated the homology between the X chromosomes of *Drosophila subobscura* and *D. melanogaster* he focused his paper more on the differential effects of X-rays on the two species.

#### 5.4.1.4 Chromosomes in *Drosophila* Races

Homology research tried to establish the evolutionary relationship between different species of *Drosophila* by comparing their chromosomes. Koller performed similar research at the DoZ/B, comparing the chromosomes of *Drosophila* races to see how their chromosomes differed.<sup>1047</sup> Koller, however, used cytological methodology.

The methodology Koller used was to compare the structure and behaviour of the normal, and the giant salivary gland, chromosomes of twelve races of *Drosophila pseudo-obscura*, and their hybrids, during meiosis and mitosis. The methodology was typically cytological. Koller made slides of the tissues studied and observed them through a microscope.<sup>1048</sup> He then made illustrations of what he saw, and fitted the drawings together to re-create the processes of mitosis and meiosis. Finally, he compared the structures and processes he observed.

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<sup>1046</sup> Christie, 1939/1940.

<sup>1047</sup> Koller, 1936b. See also Summary of Work in Progress, 3 October 1934, f578, b45, s401D, RG1.1, RFA.

<sup>1048</sup> Koller, 1936b and Koller, 1934, 67-68.

Koller's work demonstrated structural differences between the chromosomes of the *Drosophila pseudo-obscura* races. This he argued, should be expected to reduce the crossing-over frequency in hybrids, which would lead to the chromosomes of each race becoming genetically isolated and would help them to form separate races. He pointed out that the races were partially inter-sterile, backing up his hypothesis. Koller therefore used his cytological findings of structural differences between the chromosomes to deduce genetic consequences: a reduction in crossing-over.

#### **5.4.1.5 Genetic Topics in Conclusion**

This section has shown that it was common practice for the DoZ/B to use both genetic and cytological methodology when studying genetic topics in the area of chromosomal studies. However, only Koller was trained in the use of cytological methodology. This meant that the geneticists had to draw on the skills of other people to investigate their problems using both methodologies. The fact that they did so indicates a culture of working as a group at the DoZ/B.

When researching genetic topics in the area of chromosomal studies, only genetic methodology was used at the IAG. As for the DoZ/B, the geneticists who performed this work were not trained in the use of cytological methodology. However, they worked alongside people who were. This suggests that there was a barrier between these geneticists and the cytologists or a culture of individuality at the IAG.

#### **5.4.2 Cytological Topics**

In this section I investigate the methodology and aims of the one cytological topic to be researched at the two locations: how X-rays cause gross structural changes to chromosomes. This demonstrates once more, that only one approach (genetical or cytological) tended to be used at the IAG. However, since the

research was conducted at the IAG by a research group led by H.J. Muller<sup>1049</sup> it also suggests that this was not due to a culture of individuality.

In 1937 Muller joined the IAG.<sup>1050</sup> Fairly quickly a group gathered around him, all working to investigate mutagenesis.<sup>1051</sup> Muller co-ordinated the work of the group such that they carried out a detailed investigation of the method by which X-rays affected the chromosomes to cause structural changes.<sup>1052</sup> Their work was exemplary of the type of research programme I described the RF promoting in Chapter Three (section 3.2). Their organisation was also the one that the RF promoted. Muller worked out the theory and thus what experiments needed to be conducted, his team carried out the research work.

The aim of the group's research was to decide between two theories of how structural changes, caused by radiation, occur in chromosomes. This research topic was cytological because it studied structural changes in the chromosomes. The two theories of how the changes occurred were firstly, that the chromosomes that exchanged connections came into contact and then broke and secondly, that the chromosomes broke first and then re-connected with other broken ends.

The normal method of testing the theories was to calculate how the proportion of structural changes varied with radiation dosage. However, the variation seen for gross rearrangements was not that expected for either theory. Muller and his colleagues therefore tested various factors to see whether they also influenced the proportion of gross rearrangements that occurred in a population. The method they used was to vary the factors while radiating adult male *Drosophila* with a fixed dose of radiation. The radiated males were then mated and the phenotypes of the offspring observed to see whether a translocation had occurred or a lethal factor arisen. This methodology was typically genetic; breeding organisms and studying the offspring's phenotype. Genetic methodology was therefore used at the IAG to investigate a cytological topic and decide between two cytological theories.

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<sup>1049</sup> See for example, Muller, Makki and Sidky, 1938/1939.

<sup>1050</sup> Crew to Sir, 17 February 1938, f44, b4, s405D, RG1.1, RFA.

<sup>1051</sup> Carlson, 1981, 251, 260.

<sup>1052</sup> Muller, 1940.

This methodology was seen throughout the group's work. For example, as the results showed that other factors had no effect on rearrangement rate, Muller tried to account for the aberrant change in the rate of gross rearrangements. He postulated that the rate seen was between that expected on either theory, either because both occurred to some extent or because the breakage first theory held but not all rearrangements were visible because multiple rearrangements occurred in the same chromosome. Muller tested this by radiating adult male *Drosophila* at low dosage, when multiple rearrangements should occur less frequently. He then bred the males with females and studied the phenotypes of the offspring to see how many translocations had occurred.

This section demonstrates that there were intrinsically cytological topics in the area of chromosomal studies. These were not investigated at the DoZ/B. They were only investigated at the IAG following the arrival of Muller. However, once a cytological topic was studied, it became one of the Institute's major research topics. Muller used genetic methodology to investigate the topic, which was possible because structural changes to the chromosomes had genetic implications. Cytological methods were not used. However, the research programme was investigated by a group of researchers. This suggests that the barrier to using multiple methodologies was not a culture of individuality.

### **5.4.3 Cytogenetic Topics**

In this section I investigate the aims of the cytogenetic topics investigated at the DoZ/B and the IAG, and the methodology used to study them. I show that the locations differed in the extent to which they researched such problems and the methodology they used.

#### **5.4.3.1 Chiasmata and Crossing-over**

One of the major cytogenetic topics researched at the IAG during the 1930s was the relationship between the cytological phenomenon of chiasmata and the

genetic phenomenon of crossing-over. The topic was cytogenetic because it investigated the relationship between genetics and cytology.

At the start of the 1930s there were two theories of the relationship between chiasmata and crossing-over. In 1930 Karl Sax postulated that crossing-over occurred when a chiasma breaks.<sup>1053</sup> The more crossing-over that occurred the less chiasmata should be observed, because they broke to allow crossing-over. However, in 1931 Cyril Darlington postulated that chiasmata resulted from crossing-over.<sup>1054</sup> The more crossing-over there was the more chiasmata should be observed. Thus, the frequency of chiasmata and crossing-over correlated negatively on Sax's theory and positively on Darlington's theory.

In 1932 Crew and Koller published a paper regarding their investigation of the two cytogenetic theories.<sup>1055</sup> The methodology employed was to take smears of testicular tissue from 1-3 day old mice and stain them. Hair follicles of the same mice and tumour tissue were also taken and embedded into wax. This was sectioned before staining. The samples were observed under a microscope and drawings made. The pair described the structure of the chromosomes and their behaviour at different stages of division. Since the pair had static pictures taken at different times during the process of cell division, the process had to be constructed. This was done by referring to the accepted stages a cell passes through during mitosis; in other words by referring to cytological theory. The length of each stage was also established, presumably by comparing the number of cells observed to be in each stage of division. Meiosis was followed in the testicular tissue by reference to the partial chiasmotype hypothesis, a cytogenetic theory, and the number of chiasmata was observed. The methodology was thus cytological, though based on both cytological and cytogenetic theory.

Crew and Koller compared the number of chiasmata at different stages of division in males and females. They then compared the difference in chiasma

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<sup>1053</sup> Sax, 1930, 216-217.

<sup>1054</sup> Darlington, 1931, 257.

<sup>1055</sup> Crew and Koller, 1932.

frequency they had established between the genders with the difference in crossing-over frequency given in the literature.

Crew and Koller found that females show more chiasmata than males. The literature also showed that females undergo more crossing-over. The pair pointed out that this supported Darlington's contention that chiasmata are the result of crossing-over and did not support Sax's alternative hypothesis. By using cytological methodology and the results of others' work done with genetic methodology, the pair therefore made a cytogenetic conclusion.

No similar studies were conducted at the DoZ/B. This section demonstrates once again the use of a single methodology to study chromosomal genetics at the IAG. The results of Koller and Crew's cytological work were compared to genetic results in the literature. The fact that the results were in the literature may explain in this case why both methodologies were not used. This case appears to cast doubt upon the hypothesis of a barrier between the Institute's geneticists and cytologists. Koller was primarily a cytologist and Crew a geneticist. However, Crew appears to have put his name on papers that he did very little work on.<sup>1056</sup> This was certainly true of work done by Koller, who wrote to Darlington:

“...he [Crew] had five papers in the Journal and I wrote three of them, the authors were Crew and Koller.”<sup>1057</sup>

#### 5.4.3.2 The Sex Chromosomes

Another major topic of cytogenetic research at the IAG was the investigation of the sex chromosomes. The sex chromosomes posed a problem for attempts to synthesise cytological and genetic theory. In 1931 Cyril Darlington suggested that chiasmata, a cytological phenomenon, were necessary for chromosomal pairing and that they resulted from genetic crossing-over.<sup>1058</sup> This raised the question of how the sex chromosomes remained genetically differentiated from each other. The differentiation was thought to be maintained by the

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<sup>1056</sup> Beale, 1995, 26.

<sup>1057</sup> Koller to Darlington, 5 March 1940, folder J.133, box c.110, Darlington papers.

<sup>1058</sup> Darlington, 1931, 257.

chromosomes having two regions: a pairing segment and a differential segment, which was completely sex-linked. The arrangement of these regions was not fully established in the early 1930s.<sup>1059</sup> The investigation of the sex chromosomes was therefore a cytogenetic problem that arose from attempts to synthesise cytological and genetic theory.

In 1934 Koller and Darlington published a paper on the genetics and behaviour of the sex chromosomes in the rat.<sup>1060</sup> Testicular material was fixed, embedded in paraffin, stained and sectioned. The slides were then observed under the microscope. The process of meiosis was observed and the pairing of the sex chromosomes. The methodology used was therefore cytological. In reconstructing the process of meiosis a cytogenetic theory was used.

Koller and Darlington found that chiasmata only formed in certain regions of the sex chromosomes in Norway rats. Using the theory that chiasmata result from crossing-over, they concluded that the sex chromosomes had differential and pairing segments in both the X and Y chromosomes.

Koller and Darlington's collaboration was followed by a number of studies of sex chromosomes conducted by Koller alone. One of these, on *Macacus Rhesus*, was conducted at the DoZ/B,<sup>1061</sup> the rest were conducted at the IAG. Subsequent papers aimed to provide further evidence for the differential structure of, and method of pairing in, the sex chromosomes.<sup>1062</sup> These studies did not differ significantly from that discussed above. Again, only cytological methodology was used in these investigations, as shown in section 5.4.3.3, a genetic approach was also possible.

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<sup>1059</sup> Koller and Darlington, 1934, 159.

<sup>1060</sup> Koller and Darlington, 1934.

<sup>1061</sup> Summary of Work in Progress, 3 October 1934, f578, b45, s401D, RG1.1, RFA. See also Miller's diary, October 22, 1934, RG12.1, RFA.

<sup>1062</sup> See for example, Koller, 1936c and Koller, 1938a.

#### 5.4.3.3 Crossing-over between the X and Y Chromosomes

A similar cytogenetic problem to that described in section 5.4.3.2 was investigated at the DoZ/B using genetics methodology. Specifically, Philip tackled the problem of crossing-over between the X and Y chromosomes of *Drosophila melanogaster*.

In her paper on the subject,<sup>1063</sup> Philip couched the problem in genetic and cytological terms. She discussed the fact that crossing-over had been observed in male *Drosophila*, though it was rare. Thus, chiasmata must be formed. Philip therefore followed Darlington in relating a genetic phenomenon (crossing-over) to a cytological phenomenon (chiasmata). Crossing-over between the X and Y chromosomes had been observed in attached X stocks, but not in XXY stocks. Philip aimed to demonstrate that it occurred in them by using stocks with high secondary non-disjunction, caused by an inversion in the X chromosome, presumably that described above. The methodology Philip used was genetic. She crossed large numbers of *Drosophila melanogaster* whose genotype was designed to reveal when crossing-over occurred.

Philip found that all the crossing-over was double. This, she pointed out, supported Darlington's contention that double crossing-over was the normal form because the chromosomal structure, with two complexes in the Y chromosome, could not be maintained with single cross-overs. Philip therefore used genetic methodology to support the genetic element of a cytogenetic theory. This work was done alongside the cytological work of Koller on the sex chromosomes of *Macacus Rhesus* at the DoZ/B, described above. Once again, both genetic and cytological approaches were used to the same problem at the DoZ/B.

#### 5.4.3.4 Asynapsis

In this section I show that cytogenetic problems could arise from breeding concerns. Cytogenetical work therefore was not solely academic in nature. From

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<sup>1063</sup> Philip, 1935.



1936 Koller investigated sterile *Pisum* plants to see whether the sterility was caused by genetic or cytological factors.<sup>1064</sup>

Koller used cytological methodology to study the sterile *Pisum* plants. He fixed root tips from the plants, sectioned and stained them. He then observed the slides he had created with a microscope and drew what he observed. Mitosis was studied in sixteen plants and meiosis in five.

Koller discovered that the chromosomes of sterile plants failed to pair during the metaphase stage of meiosis. Koller argued the failure could be due to structural changes in the chromosomes, the number of chromosomes being different, or genetic control. Koller found evidence in favour of all three in different *Pisum* plants. Koller suggested that genetic factors caused the chromosomes to split early. He argued that this prevented chiasmata formation because chiasmata form at the moment of splitting. The failure to form chiasmata prevented chromosome pairing, leading to irregular segregation of the chromosomes and thus microspores with the wrong number of chromosomes.

Sterility is therefore shown not to be a cytological or genetic problem. It could arise from the plants' genetics, cytology, or, as Koller postulated, a mixture of both. He investigated the problem cytologically and identified some cytological causes. However, these could not fully explain the sterility alone so he postulated additional genetic causes.

#### **5.4.3.5 Cytogenetic Topics in Conclusion**

Cytogenetic topics were far less studied at the DoZ/B than the IAG. However, at the DoZ/B these topics were simultaneously studied with both cytological and genetic methodology. Koller and Philip both studied the relationship between pairing, chiasmata and crossing-over in the X and Y chromosomes. Koller did so with cytological methodology, Philip with genetic methodology.

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<sup>1064</sup> Koller to Darlington, 1 November 1936, folder J.125, box c.110, Darlington papers. Koller, 1938b.

The extent of research on cytogenetic topics conducted at the IAG far exceeded that conducted at the DoZ/B. That was due to the extensive research which was done at the IAG on the sex chromosomes and on the relationship between chiasmata and crossing-over. Cytological methodology was exclusively used at the IAG to study cytogenetic topics.

#### **5.4.4 Chromosomal Studies in Conclusion**

Section 5.3 showed that chromosomal studies were conducted in both the breeding and academic settings for genetics. However, this section has demonstrated that there was a clear difference between the research topics in this area that were studied at the DoZ/B (in the academic setting) and the IAG (in the breeding setting). Genetic topics were studied at both locations to a similar extent. Cytological topics were only studied at the IAG. Cytogenetic topics were studied at the IAG to a far greater extent than at the DoZ/B. The main focus of chromosomal studies at the DoZ/B was therefore genetic topics. This compared with a main focus on cytogenetic topics at the IAG prior to 1938, after which cytological topics became the most studied area of chromosomal research at the Institute.

The difference in topics studied can be explained by the differential skills researchers had at the two locations. Only Koller was trained in cytological methodology at the DoZ/B and he only worked there briefly.<sup>1065</sup> The projects were therefore set by geneticists, and so were genetic in nature. It also resulted in genetic methodology predominating at the DoZ/B. A number of researchers carried out cytological work at the IAG (Koller, William Bryden, H.D. Slack). Since these researchers almost always worked in the field of chromosomal studies, and the Institute's geneticists worked on other fields too, the work of cytologists dominated the field of chromosomal studies at the IAG. This led to a predominance of cytogenetic topics at the IAG, prior to Muller's arrival. This also meant that cytological methodology predominated at the IAG, until 1938 when genetic methodology became predominant.

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<sup>1065</sup> Emmens appears not to have been part of the research group, but was brought in to do the cytological work Grüneberg needed to be done.

The researchers had differential skills at the different locations because of the locations' settings. In 1932 the sub-committee who inspected the IAG on behalf of the ARC reported:

“It seems doubtful whether the staff possess a competent cytologist.”<sup>1066</sup>

The ARC's recommendation that a cytologist was employed led to Koller's employment in 1933.<sup>1067</sup> The ARC wanted a cytologist on staff because there was a cytological aspect to breeding, as shown by Koller's work on asynapsis in peas. Though not all the work Koller performed had a breeding aspect to it, it was performed at the IAG because it was of interest to a cytologist and the ARC wanted a cytologist on the Institute's staff because cytology was an aspect of breeding.

A cytologist, M.J.D. White, was also employed at the DoZ since cytology was an aspect of zoology. However, he never became part of the genetics group because he was not interested in evolutionary genetics.<sup>1068</sup> Haldane appears to have been interested in having a cytologist in his group. As seen in Chapter Two (section 2.2.3) Haldane wanted to retain Koller. He also asked White to join his group.<sup>1069</sup> Haldane could not recruit a cytologist because, as discussed in Chapter Three (section 3.3.1.1), he did not have funding to pay them a salary. The lack of funding available in the academic setting therefore prevented Haldane from forming a research programmes involving both cytology and genetics. This confirms the findings of section 5.3 above.

Another finding of this section was that genetic and cytological methodologies were only used to tackle the same problem at the DoZ/B and not at the IAG. This suggests that there was a culture of working as a research team at the DoZ/B and a culture of working alongside each other at the IAG. This was probably due to the difference in size of the two locations. The DoZ/B was small enough for all

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<sup>1066</sup> A8, folder Memos, financial reports, IAGA.

<sup>1067</sup> Minutes, 11 October 1933, folder Minutes, IAGA.

<sup>1068</sup> Peacock and McCann, 1994, 406.

<sup>1069</sup> Peacock and McCann, 1994, 406.

the geneticists to work as a group and know about each other's work. The IAG had to be organised into groups. These groups separated genetics from cytology and thus the methodology of each discipline were not combined to tackle the same problem. This difference was once again due to the different amount of funding available in the two settings.

## **5.5 Conclusion**

Problem choice differed in the breeding and the academic settings. In the breeding setting it involved a choice of both research area and organism. In the academic setting it only involved a choice of research area.

As well as problem choice differing between the settings, choice of research area was motivated by the setting in which the research was conducted. In the breeding setting transmission genetics was generally studied alongside other approaches to the problem of breeding, such as physiology and cytology. An integrative synthesis only occurred with cytology, which was also studied in its own right. In the academic setting, in contrast, there was a culture of synthesising genetics with other disciplines. In zoology departments this tended to be evolutionary studies; in botany departments it tended to be cytology. An integrative synthesis of genetics and other disciplines therefore occurred to a greater extent in the academic setting than the breeding setting.

The main areas of overlap between the settings, in terms of research area, were cytogenetics and transmission genetics. Section 5.3.3 suggested that such work was linked to theory in the academic setting far more than was the case in the breeding setting. Cytological methodology was also used far more extensively in the breeding than the academic setting. In terms of synthesis, breeding locations tried to synthesise theory, while academic locations synthesised methodology.

## Chapter Six

### Conclusion: Settings for Genetics in 1930s Britain

#### 6.1 Introduction

In this chapter I consider the contribution my dissertation has made to knowledge. I discuss the data collection that has been conducted in section 6.2, and, in sections 6.3-6.5, I bring together the arguments made in Chapters Two to Five to demonstrate my three theses. In doing so, I demonstrate that the new concept I introduced in this thesis, ‘setting’, is a useful heuristic for understanding the history of British genetics. Finally, I discuss other conclusions and research questions that have arisen during the course of my work, in sections 6.6 and 6.7.

#### 6.2 Empirical Research

Prior to this dissertation little research had been done on genetics in 1930s Britain. In Chapter One (section 1.8) I showed that most of the secondary literature on British genetics focused on great geneticists and great discoveries. This meant there was no map of British genetic locations. The names of locations had to be gained from scientific articles, biographical memoirs and archival material. The geneticists who worked at them, the type of research conducted, and the extent of it, were all obtained in the same way.

One British geneticist that had been extensively studied was J.B.S. Haldane. However, the context of his work, the DoZ/B, had not previously been studied.<sup>1070</sup> My findings regarding the DoZ/B are therefore based entirely upon archival research and published scientific papers.

The IAG had a better presence in the secondary literature. Some of the Institute’s research was discussed in Sturtevant’s intellectual history of genetics;<sup>1071</sup> Crew

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<sup>1070</sup> A brief mention of the Department’s work is in Adams, 1968.

<sup>1071</sup> Sturtevant, 1965.

had written recollections of the IAG;<sup>1072</sup> brief histories also exist on the internet<sup>1073</sup> and in the Institute's archives. Amongst the latter, Deacon<sup>1074</sup> provides a good framework for understanding the history of the Institute. However, most of the detailed information about genetics at the Institute had to be gained from archival material and published scientific papers.

### 6.3 Thesis One

In this section I consider the evidence that has been provided by this dissertation for my first thesis: that during the 1930s, genetics in Britain grew most rapidly in the medical and breeding settings and least rapidly in the academic setting, relative to their original sizes. As stated in Chapter One (section 1.1) this involved three stages. I show that all three stages were demonstrated in my dissertation and thus so was thesis one.

The first stage was to establish that genetics in Britain was growing. Lewis had previously shown that membership of the British Genetical Society grew by approximately 25% (from circa 120 members to circa 150 members) between 1936 and 1939.<sup>1075</sup> This demonstrated a growth in interest in genetics during the 1930s, and suggested a growth in research. In addition, in Chapter Two (section 2.4) I demonstrated a growth in the number of researchers studying genetics during the 1930s. I found that during the 1930s approximately forty more researchers studied genetics than during the 1920s. This represented an increase of 100% in the number of British geneticists between the 1920s and 1930s.

The second stage was to show that genetics was studied in different settings in 1930s Britain. Rosenberg had previously suggested that there were different contexts for genetics research in America. However, he provided little evidence to support his contention. Other historians<sup>1076</sup> have focused on the work of institutes that can be categorised into the breeding or academic settings.

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<sup>1072</sup> Crew, 1971.

<sup>1073</sup> McKeen, 2002. Bulfield, 1999.

<sup>1074</sup> Deacon, unpublished.

<sup>1075</sup> Lewis, 1969, 4-5.

<sup>1076</sup> See, for example, Harwood, 1993, 197-225; Kimmelman, 1992.

However, no explicit discussion of settings had been conducted prior to this dissertation. Chapter Two demonstrated that the concept of setting is a feasible heuristic by categorising locations into settings. Chapters Three to Five showed that the concept is analytically useful by demonstrating that when the funding, research organisms and problems of different locations are considered, the locations tend to form clusters. These clusters coincide with settings. Thus, genetics can be usefully considered to have been studied in different settings in 1930s Britain.

The third stage was to prove that genetics grew most rapidly in the medical and breeding settings and least rapidly in the academic setting, relative to their original sizes. In Chapter Two (section 2.4) I showed that the medical setting effectively emerged during the 1930s. At the start of the decade there were no genetic locations or researchers in the setting. By the end there were four locations and five geneticists in the setting. The breeding setting approximately doubled in terms of both locations and geneticists during the 1930s. It increased from twenty four to fifty six geneticists and six to eleven locations. The academic setting also grew in terms of researchers. However, its growth was less than the other settings, at about 50%, and it did not grow in number of locations.

The medical and breeding settings for genetics therefore grew in terms of both number of locations and researchers. The academic setting grew in terms of number of researchers, but not locations.

There are a number of methodological constraints upon this conclusion. Firstly, geneticists were defined as authors of more than one article in the *Journal of Genetics* during the decade. If another definition had been used the findings may have been slightly different. Many of the new breeding locations for genetics in the 1930s had had genetics research conducted at them in the 1920s, but they did not classify as locations at that time because none of the researchers published twice in the *Journal*. The growth in terms of researchers seems unlikely to have been affected, however, since the definition of a geneticist was consistent across the decades. Another constraint this methodology places on the conclusion is that

I was dependent upon the *Journal's* definition of what was genetics, rather than using my own, as laid out in section 2.4.1.2.

## 6.4 Thesis Two

My second thesis was that there was a 'type' of genetics associated with each setting. I defined 'type' as a configuration of 'defining characteristics'. The latter were defined as types of a characteristic of genetics, such as a type of funding, type of research organism, or type of problem. In this section I describe the 'type' of genetics associated with the breeding and academic settings.

In Chapters Three to Five, I demonstrated that the type of genetics associated with the breeding setting was composed of DC/ARC recurrent funding and the receipt of external funding. Control over the content of the research lay primarily with the funding bodies. Research organisms were domesticated and used as physical models of groups low down the is-a hierarchy. Information about the group 'organisms' was gained by using different organisms as instances of the type group 'organisms', rather than as a model of the group. Organisms tended not to be treated as research tools. Research areas studied were cytology, transmission genetics and cytogenetics.

The type of genetics associated with the academic setting was composed of recurrent funding solely from a university and minimal amounts of soft money, mainly given to individuals. The funding bodies did not try to influence the specific content of the research done. Instead they encouraged broad research and left control of the specifics to the locations' geneticists. Research organisms were domesticated plants, wild animals, or artificial animals. These were used to provide information about organisms in general, either through instances of 'organisms' or using the research organisms as physical models of the type group 'organisms'. Organisms tended to be used as research tools. The areas of research investigated were evolutionary genetics, cytogenetics and transmission genetics.



While these types of genetics were associated with the academic and breeding settings, the strength of the association between the settings and the different defining characteristics varied. This variation is described and accounted for in section 6.5. For now it is only important to note that the defining characteristics did not define setting. Domesticated plants, for example, were used as research organisms in both settings.

No comparison of genetics in the academic and breeding settings has previously been conducted. However, Harwood has compared early Twentieth Century genetics at the Institute of Zoology in Göttingen and at the Berlin Agricultural College.<sup>1077</sup> The former can be considered a location in the academic setting, the latter a location in the breeding setting. Harwood found that different bodies supported genetics at the two locations. The Berlin Agricultural College received substantial government and industry funding, while the Institute of Zoology received little money from these sources. The Berlin Agricultural College researched pure and applied genetics, focusing the former on transmission genetics. The Institute of Zoology only researched pure genetics, focusing on developmental genetics. This suggests that my findings are applicable outside of Britain.

The methodological constraints upon thesis two are that only one location in each setting was studied in detail. Surveys were conducted to indicate the applicability of findings for the two locations to their respective settings. These surveys revealed that the IAG was slightly unusual in that it conducted both breeding and academic genetic activities. Findings based solely on the IAG, such as the case studies, therefore need to be treated with care. While the surveys could reveal how representative the locations were, they did not have sufficient depth to account for the differences. Some differences existed between all the locations. This means that the ‘types’ of science outlined above are guides to the genetics conducted in different locations, based upon setting; they are not rules.

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<sup>1077</sup> Harwood, 1993, 197-225.

## 6.5 Thesis Three

My third thesis is that the characteristics of science interacted in such ways that the types of genetics found in the different settings were stable. In this section I discuss the mechanism by which the defining characteristics of each setting interacted to create stability.

Of the defining characteristics funding, especially recurrent funding, was most strongly associated with setting in 1930s Britain. The aims of academia were embodied in the universities and the aims of breeding in the DC/ARC. This did not exclude other bodies from embracing these aims and providing funding to forward them. Other bodies rarely provided recurrent funding because of the amount of money that was required to maintain an institution. However, it occasionally occurred. For example, the JI received its recurrent funding from the endowment provided by John Innes's Will.

Recurrent funding bodies controlled the context locations provided for work. For example, the DC set up an Animal Breeding Research Department at Edinburgh. Even after it had changed its name, the location still directed its research towards animal breeding. Universities also controlled the context of research by employing geneticists in botany, zoology or genetics departments. The context influenced the research problems tackled. At the DoZ/B, for example, research was conducted to throw light on the relationship between the structure and function of animals.

Recurrent funding bodies had tighter control over the research conducted in the breeding setting than in the academic setting. One method the DC/ARC used to control research problem was to control the permanent staff employed. For example, in 1935 Crew wanted to redirect the IAG towards cytogenetics. The ARC prevented this by only agreeing to fund the employment of five researchers whose specialities were pure genetics, cytology, physiology, agricultural genetics and statistics. The presence of the latter three employees meant that the Institute could not focus solely on cytogenetics. Another method the DC/ARC used to

control research problem was to require the presence of a committee to direct breeding institutes towards breeding research. This took the power to subvert the locations' aims away from their directors.

Problem choice was also influenced by the availability of soft funding. Again, control over problem choice was tighter in the breeding setting. In that setting project-focused grants were common place. Geneticists proposed projects to funding bodies, who decided whether to fund them. The ARC, the Empire Marketing Board and the Department of Agriculture all provided money to breeding locations in this way. Project-focused grants were not a feature of the academic setting. Bodies that provided soft money to the academic setting therefore had less immediate influence over problem choice. However, they still had some influence over problem choice. The RF, for example, tended to fund long-term programmes of research, which involved a group of researchers. This organisational structure encouraged problems of wide applicability to be chosen for study, as they took longer and could employ more people. The negotiation of organisation, length, and content of research, between the RF and British geneticists was studied in Chapter Three (section 3.2). The negotiation process has previously been noted by Kohler.<sup>1078</sup> To this I have added knowledge of research features that resulted from the RF's negotiations.

The lack of control funding bodies had over problem choice in the academic setting meant that it was mainly in the hands of geneticists. As seen in Chapter Five (section 5.2.1), Haldane's vision of genetics was the most important influence over the work done at the DoZ/B. This also encouraged genetics to be synthetic in the academic setting. Very few geneticists had been trained solely in genetics because it was not well established in the academic setting prior to the 1930s. This meant they commonly had other interests, such as physiology or evolution, and used genetics to provide information about these disciplines too.

Problem choice involved selection of both research topic and organism in the breeding setting. Breeding locations investigated the genetics of a particular

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<sup>1078</sup> Kohler, 1991a.

organism, rather than the genetics of generic organisms. Thus, research organisms were usually used as physical models of groups low down the is-a hierarchy.

In the breeding setting, research organism was controlled as tightly as research topic by the DC/ARC because both formed part of problem choice. Palladino has described how the DC resisted calls for new Plant Breeding Stations as it feared their functions would overlap. Palladino wrote that this objection was overcome by restricting all the Plant Breeding Stations to researching locally important crops.<sup>1079</sup> To prevent overlap across the entire breeding setting, the DC/ARC had to retain control of the organisms used for research.

Research organism was not part of problem choice in the academic setting. It could be argued that the choice between animals and plants formed part of problem choice, as zoology departments were supposed to provide information about animals and botany departments were supposed to provide information about plants. However, academic geneticists saw genetics as a unifying force across the zoology/botany divide. In 1936 eight geneticists wrote to *Nature*:

“Nuclear division and sexual heredity are the same in principle in the fly and the flowering plant. ... This view of the unity of living things in their genetical aspects is so clear and important...”<sup>1080</sup>

Any organism could therefore be used to gain information about the group ‘organisms’.

While organism choice was not part of problem choice in the academic setting it was closely related to it. In Chapters Four and Five it was demonstrated that some organisms are more suitable for certain types of work. Haldane argued that inbred mice were the most suitable organism for cancer research. In practice, his group used mice for physiological and developmental genetics and *Drosophila* for population genetics. Developmental genetics was studied because the

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<sup>1079</sup> Palladino, 2002, 46-52, especially pp.47-48.

<sup>1080</sup> Ashby, Crew, Darlington, Ford, Haldane, Salisbury, Turrill, Waddington, 1936.

department's mice suffered a developmental mutation. Here organism choice influenced problem choice. However, problem choice could also influence organism choice. In the case of serological genetics, Gorer switched from fowl, which he used at the JI, to inbred mice because they were more suitable for the work.

Organism choice, and thus problem choice, could also be influenced by funding in the academic setting. The lack of funding Haldane had encouraged the use of *Drosophila* because it was inexpensive. *Drosophila* was more suitable for population genetics than physiological genetics, which were Haldane's two main interests, and so his group focused on this area of research.

Problem choice was also associated with the use of organisms as research tools. When the problem pre-dated the choice of organism, the organism tended to be used as a research tool. This was seen more in the academic setting. In this setting, information was sought about genetics in general. The emphasis was therefore on research problem, not research organism. In the breeding setting, research problems tended to arise from organisms. The problem therefore related to the organism itself, which could not therefore be used as a tool to investigate an abstract problem.

This section has shown that the breeding and academic settings did not just differ in the type of genetics associated with them, but in the relationships the characteristics of genetics had to each other.

In the breeding setting the recurrent funding body, the DC/ARC, had tight control over problem choice, which involved both choice of research organism and research topic.

In the academic setting the recurrent funding bodies, the universities, had less control over research topic and research organism. They could influence problem choice by providing certain contexts for the research. They could influence organism choice by the level of funding they provided. Research organism and research topic also influenced each other in the academic setting. The latter was

possible because the information sought regarded generic 'organisms'. The best physical model for 'organisms' was therefore desired, rather than a particular organism to provide information about a group low down the is-a hierarchy.

Stability in the defining characteristics of genetics was seen in the breeding setting because the DC/ARC had a strong influence on research topic and problem choice. It was also seen in the academic setting because funding influenced research topic and research organism, and the two interacted with each other.

The methodological constraints upon these conclusions are the same as those upon thesis two. The major constraint being that the findings are mainly based upon a comparison of two locations.

## **6.6 Other Conclusions**

In the course of my dissertation I have also investigated the implementation of philanthropy by the RF, the concept of model organisms and the concept of the right tool for the job. In this section I discuss the way my dissertation has made a contribution to the literature on these subjects.

In Chapter Three (section 3.2) I showed that the RF was interested in funding academic genetic activities. Within these bounds the Foundation portrayed themselves as uninterested in the specifics of the research. This was presumably because it was necessary for the RF to portray itself as a benign organisation.<sup>1081</sup> The RF, however, promoted an organisational structure where researchers worked co-operatively on a long-term project. This favoured work of wide relevance, and thus synthetic rather than transmission genetics. Zallen has previously noted that the RF promoted interdisciplinary work, though she accredited this to its American values.<sup>1082</sup>

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<sup>1081</sup> See Karl and Katz, 1987.

<sup>1082</sup> Zallen, 1989.

The RF placed great importance on stability and reputation. The latter has previously been noted by Abir-Am.<sup>1083</sup> I claim that it provides an explanation for the appearance that the RF promoted American values. The RF was dependent upon *American* geneticists for opinions as to who was worth backing. The RF was also keen to fund in a situation where another funding body was likely to take over responsibility for supporting the work. This allowed them to support innovative rather than everyday science.

My research on the RF illustrated the surveillance that the Foundation carried out to discover who was worthy of their support. One of the interesting findings of this work was that the RF valued Crew's opinions of other geneticists even though they evaluated his work as being of insufficient quality for their support. An explanation for this comes from a Foundation officer's impression that:

“genius though Crew be, his energies are frittered away with things far beneath his ability.”<sup>1084</sup>

The research also provided new insights into the characters of Haldane, Watson and their relationship. Haldane has a reputation for being forthright.<sup>1085</sup> In his initial interactions with the RF he was remarkably cautious. Watson is best remembered for his palaeontology research but he was prepared to take time from this to do the necessary administration to ensure Haldane's group had a secure position at the College. In an obituary of Watson it is noted:

“It was often a source of wonder to visitors that Haldane and Watson, both men of powerful personality and very different temperament, did not clash in some spectacular fashion. In fact they held one another in high regard because of the complementarity of their personalities and abilities.”<sup>1086</sup>

My findings fully support this contention.

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<sup>1083</sup> Abir-Am, 1982.

<sup>1084</sup> Tisdale to Weaver, September 24, 1934, f44, b4, s405D, RG1.1, RFA.

<sup>1085</sup> See for example, Pirie, 1966, 237.

<sup>1086</sup> Parrington and Westoll, 1974, 487.

Chapter Four adds to the concept of model organisms by showing that it is a special case of physical modelling. I show that research organisms are usually used as physical models for a group of organisms. All that differs between using an organism to gain information about their species and as a model organism is the size of the group modelled.

Chapter Four also adds to our understanding of the ‘right tool for the job’ thesis. Epistemologically an organism is exactly right tool for the job when modelling a group low down the is-a hierarchy. For example, a cow is exactly the right tool for the job when information is required about generic cows. Epistemologically an organism is the best tool for the job when the group being modelled is high up the is-a hierarchy. *Drosophila* may be the best tool for population genetics, but it is not the only organism that can be used to provide information about the group ‘organisms’. When the ‘right tool for the job’ thesis is used in its epistemological sense it therefore only has explanatory value where the group modelled is high up the is-a hierarchy. This occurs where problem choice is primarily a matter of research topic choice and not organism choice. My dissertation shows that this was the case in the academic setting, but not in the breeding setting. The thesis still has explanatory value in the breeding setting, because an organism can sociologically be the ‘right tool for the job’. Kimmelman,<sup>1087</sup> for example, has shown that maize was sociologically the right tool for R.A. Emerson in the breeding setting.

One of the interesting findings of Chapter Four was Haldane’s shift, from strongly supporting the use of inbred mice for research, to minimising their use in his group’s work. This shows the concept of ‘rightness’ being redefined. Originally inbred mice were the right tool for controlling the genotype of the organisms used for research. Later they became the wrong tool for providing results that were generally applicable to all organisms.

One of the curious findings from Chapter Five was that Muller managed to succeed in redirecting the IAG towards cytogenetics, where Crew failed. Power

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<sup>1087</sup> Kimmelman, 1992.



over research conducted at the IAG therefore came more from Muller's reputation and thus ability to gain funding and inspire confidence in postgraduates than from Crew's position as Director. This confirms my findings that the main power in the setting came from funding, and illustrates result of the DC/ARC attempts to minimise the power of its locations' directors.

My finding that setting influenced the type of research geneticists conducted has implications for intellectual histories of genetics. Such histories are still valid in the light of my findings. The findings they describe raised questions that later geneticists investigated. In some cases, they also offered new methods by which genetic questions could be tackled. My work does not deny that geneticists drew on past work and traditions. However, there were numerous research areas and approaches in each of them that could be drawn upon. Personal interest had a part to play, but my work offers an additional explanation. In particular I explain why particular types of research, done with particular types of organism, were clustered at certain types of institution. For example, Scott-Moncrieff used flowers to investigate physiological genetics in a breeding setting. However, physiological genetics at the DoZ/B, in the academic setting, was performed with mice. Choice of organism is obviously important to results gained.

My findings also have an implication for histories of genetics written in terms of research area. In Britain, I found that some areas, such as transmission genetics, were researched across the setting divide. Other areas, such as evolutionary genetics, were only researched in one setting. This means that a more unified approach to evolutionary genetics would be expected in Britain than to transmission genetics. This is because the evolutionary geneticists would have experienced similar influences upon their work, while transmission geneticists in the breeding setting would have experiences different influences on their work than those in the academic setting. Whether this was actually the case requires further investigation.

## **6.7 Questions Arising from this Dissertation**

Four obvious questions arise from this dissertation. Firstly, how did the British medical setting compare to the breeding and academic settings in the 1930s? As shown in Chapter Two (section 2.4) the medical setting can be considered to have emerged during the decade. It showed the quickest growth of the three settings in terms of both locations and researchers during the decade. This leads me to question whether the medical setting had stable features and how they compared to the features of the academic and breeding settings. The data collected during this thesis regarding the medical setting is insufficient to answer such questions. However, it suggests that the medical setting was between the academic setting and the breeding setting with regard to all the characteristics of genetics studied. In terms of funding, the RF had a medical sciences division that funded medical genetic activities. In this respect the medical setting was like the academic setting. Medical genetics research was also funded by the Medical Research Council, which was the medical equivalent of the Agricultural Research Council of the breeding setting. In terms of research organism, humans and mice were dominant. Like the breeding setting, humans were used as models of a group low down the is-a hierarchy. Like the academic setting, artificial organisms (mice) were used for research. Problem choice only involved the selection of research area, like the academic setting. However, this was because the whole of the setting was interested in the genetics of humans. The desire for practical results was also like the breeding setting.

Secondly, what was the place of eugenics in the settings? Research locations that aimed to study eugenics, such as the Department of Eugenics at University College London were placed into the medical setting by definition. This placement is open to question, since the Department was recurrently funded solely by a university, which was a feature of the academic setting. However, the soft funding the Department received from the Medical Research Council suggests that this placement was correct. A finding of Chapter Four (section 4.2.2.3) was that Haldane researched eugenical questions in the academic setting. However, it would seem likely that eugenics was most studied in the medical setting. The eugenical research of Fisher and Penrose was conducted in that

setting.<sup>1088</sup> I would also expect the breeding setting to have supported eugenics research. Kimmelman found this to be the case in America.<sup>1089</sup> The resolution of the relationship between eugenics research and the settings therefore requires further research.

The third question is: How did the type of genetics associated with the British settings in the 1930s compare with type of genetics associated with the British settings in other periods? The JI, in the breeding setting, spearheaded British genetics research throughout the 1910s and 1920s. Does this mean that its research was more academic at that time, or was genetics an applied discipline in Britain during that period?

The fourth question is: How representative were the British genetic settings of the settings for genetics in other countries? In section 6.4 I showed that my findings, regarding differences in funding and problem choice between the British settings, showed similarities to the differences Harwood found between the Institute of Zoology at Göttingen and the Berlin Agricultural College. Rosenberg<sup>1090</sup> also found that genetics was synthetic in the American academic setting and that agricultural organisms were used for research in the American breeding setting. Comparison of my results with those of Harwood and Rosenberg therefore suggests that my findings have wider applicability than just the British situation.

## **6.8 Conclusion**

This dissertation has shown that genetics in 1930s Britain was not a unitary discipline. It has also shown that the concept of ‘setting’ helps one to understand and account for these differences. The concept of ‘setting’ has been developed from Rosenberg’s concept of ‘contexts’ and it has been refined throughout the dissertation. I have added to our empirical knowledge of British genetics and to the literature on the RF, model organisms and the right tool for the job.

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<sup>1088</sup> For details see Kevles, 1985.

<sup>1089</sup> Kimmelman, 1983.

<sup>1090</sup> Rosenberg, 1976. 197-207.

While my dissertation has shown that settings are a useful heuristic, it has not investigated how the different settings influenced each other. The settings did not exist in isolation from each other. Thus, for example, the ARC can be expected to have influenced the academic setting to some extent simply by affecting the breeding setting. If the genetics of a nation is to be understood, the interaction of different locations needs to be investigated. By a similar argument, the genetics of a nation such as Britain did not exist in isolation from the genetics of other countries. Research has now been done on genetics in Germany, France, Russia, Spain, Britain and America.<sup>1091</sup> If the history of genetics is to be properly understood the interaction of genetics between these nations must be investigated. Obvious times when national genetics interacted were the International Genetical Congresses. It is to be hoped that the book Krementsov is currently writing on the Seventh International Genetical Congress will begin to shed light on this process.

The Seventh International Genetical Congress, held in 1939, was also a time when the British geneticists from different settings came together. It was maybe fitting then that the Congress was held at the IAG, which, I have shown, brought together features of the breeding and the academic settings at the end of the 1930s.

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<sup>1091</sup> See for example Harwood, 1993, Burian, Gayon and Zallen, 1988, Adams, 1968 and Pinar, 2002.

**Appendix One: Plans of the Department of Zoology/Biometry**

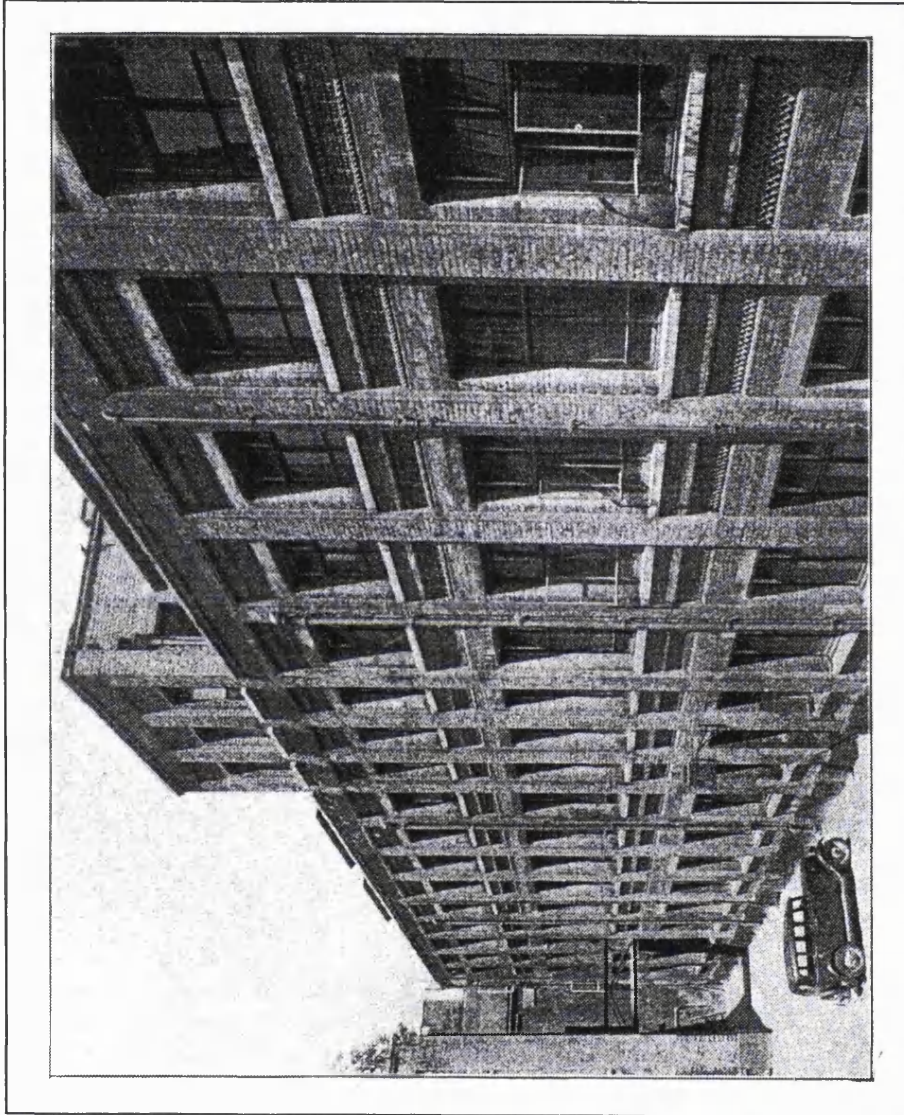
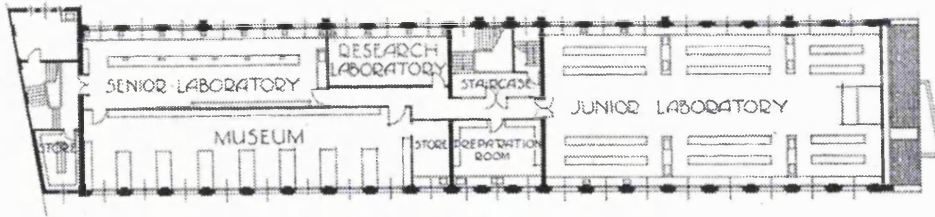
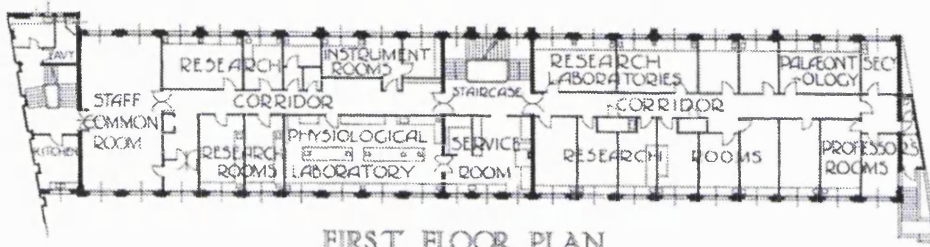


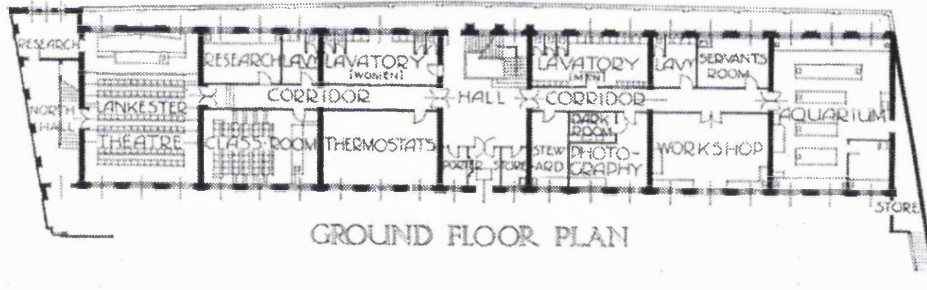
Photo of the outside of the Department of Zoology/Biometry, 1933



SECOND FLOOR PLAN



FIRST FLOOR PLAN

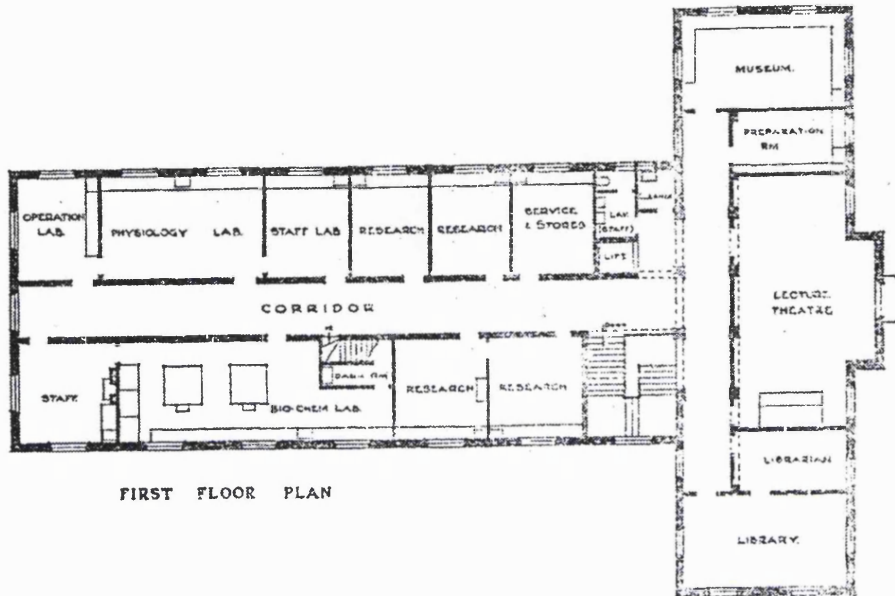


GROUND FLOOR PLAN

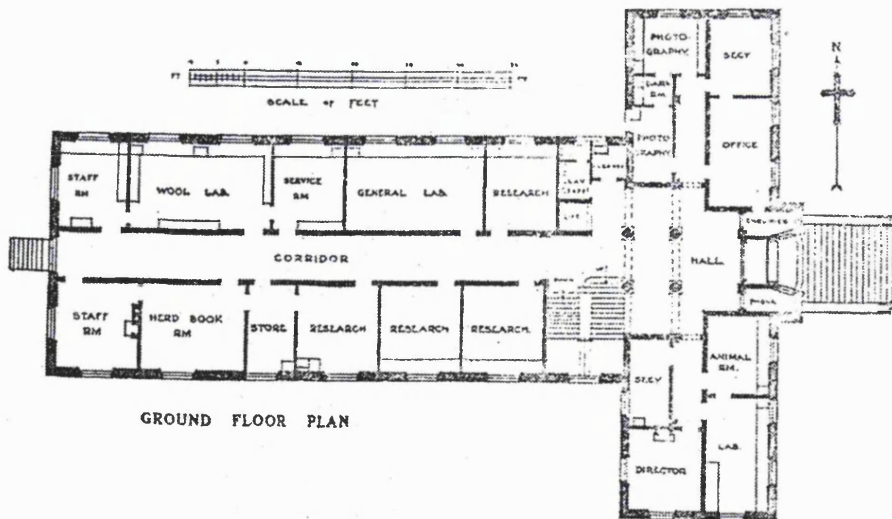
Floor Plans of the Department of Zoology/Biometry, 1933<sup>1092</sup>.

<sup>1092</sup> Photo and Plans taken from: The Department of Zoology and Comparative Anatomy, 1933.

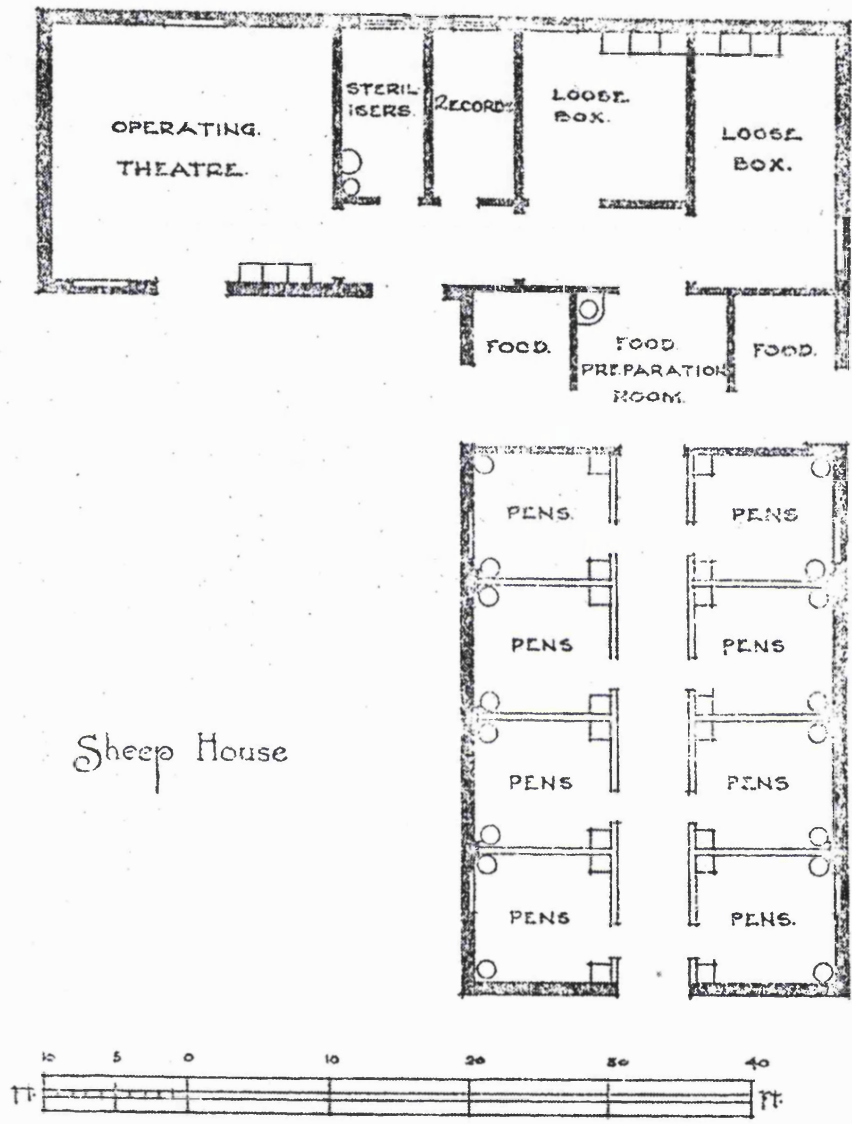
## Appendix Two: Plans of the Institute of Animal Genetics



First Floor Plan of the Institute of Animal Genetics, 1930.



Ground Floor Plan of the Institute of Animal Genetics, 1930.



Sheep House

Plan of the Sheep House at the Institute of Animal Genetics, 1930.<sup>1093</sup>

<sup>1093</sup> All Plans taken from: A7, folder Memos, financial reports, IAGA.



### Appendix Three: British Geneticists during the 1930s<sup>1094</sup>

Setting	Location	Name	Number of Publications in the <i>Journal of Genetics</i>	Membership of Genetical Society	Attended Seventh International Genetical Congress
Breeding	Jl	Haldane, J.B.S.	17	Y	Y
Breeding	Jl	Darlington, C.D.	14	Y	Y
Breeding	Jl	Mather, K.	8	Y	Y
Breeding	Jl	Lawrence, W.J.C.	8	Y	Y
Breeding	Jl	Philp, J.	8	Y	Y
Breeding	Jl	Crane, M.B.	7	Y	Y
Breeding	Jl	Upcott, M.	7	Y	N
Breeding	Jl	Gairdner, A.E.	6	Y	N
Breeding	Jl	Huskins, C.L.	6	N	Y
Breeding	Jl	Sansome, F.W.	5	Y	Y
Breeding	Jl	Scott-Moncrieff, R.	5	N	N
Breeding	Jl	Andersson-Kottö, I.	4	Y	N
Breeding	Jl	Dark, S.O.S.	4	Y	N
Breeding	Jl	De Winton, D.	3	Y	Y
Breeding	Jl	Lewis, D.	3	Y	Y
Breeding	Jl	Richardson, M.M.	3	Y	Y
Breeding	Jl	Brieger, F.G.	3	Y	N
Breeding	Jl	Moffeff, A.A.	3	Y	N
Breeding	Jl	Bartlett, M.S.	3	N	Y
Breeding	Jl	Larter, L.N.H.	3	N	N
Breeding	Jl	Tseng, H.P.	3	N	N
Breeding	Jl	Fabergé, A.C.	2	Y	Y

<sup>1094</sup> Information gathered from the Genetical Society Membership Lists 1933-1934, 1936-1939, and the *Journal of Genetics*, 1930-1939, 22-39.

Breeding	Jl	La Cour, L.	2	Y	Y
Breeding	Jl	Sutton, E.M.	2	Y	Y
Breeding	Jl	Thomas, P.T.	2	Y	Y
Breeding	Jl	Sansome, E.R.	2	N	Y
Breeding	Jl	Stone, L.H.A.	2	N	N
Breeding	Jl	Afify, A.	2	N	N
Breeding	IAG	Crew, F.A.E.	15	Y	Y
Breeding	IAG	Koller, P.C.	11	Y	Y
Breeding	IAG	Lamy, R.	8	Y	Y
Breeding	IAG	Muller, H.J.	4	Y	Y
Breeding	IAG	Greenwood, A.W.	3	N	Y
Breeding	IAG	Fraser Roberts, J.A.	3	N	Y
Breeding	IAG	Blyth, J.S.S.	3	N	Y
Breeding	IAG	Bryden, W.	3	N	N
Breeding	IAG	Cochrane, F.	3	N	N
Breeding	IAG	Donald, H.P.	2	N	Y
Breeding	Welsh Plt. Br. St.	Jenkin, T.J.	5	Y	Y
Breeding	Welsh Plt. Br. St.	Williams, R.D.	5	Y	Y
Breeding	Welsh Plt. Br. St.	Silow, R.A.	3	Y	N
Breeding	Welsh Plt. Br. St.	Ellison, W.	3	N	N
Breeding	Sch. Agr., Camb.	Watkins, A.E.	3	Y	Y
Breeding	Sch. Agr., Camb.	Howard, H. W.	3	Y	Y
Breeding	Sch. Agr., Camb.	Ellerton, S.	3	Y	Y
Breeding	Sch. Agr., Camb.	Morris, L.E.	2	Y	N
Breeding	Kew Gardens	Marsden- Jones, E.M.	7	Y	Y
Breeding	Kew Gardens	Turrill, W.B.	6	Y	Y
Breeding	Scottish Plt. Br. St.	Black, W.	3	N	Y
Breeding	Scottish Plt.	Gregor,	2	N	Y

	Br. St.	J.W.			
Breeding	Br. Res. Ass. Wool and Worsted Ind., Leeds	Fraser Roberts, J.A.	3	N	Y
Breeding	Jealott's Hill Res. St., Bracknell, Berks	Bartlett, M.S.	3	N	Y
Breeding	Amateur	Bond, C.J.	3	Y	Y
Breeding	Rothamsted	Fisher, R.A.	2	Y	Y
Breeding	Wisley Gardens	Buxton, B.H.	2	Y	N
Breeding	Sch. Agr., Uni. Coll. North Wales	White, R.G.	2	N	Y
Academic	DoZ/B, UCL	Haldane, J.B.S.	17	Y	Y
Academic	DoZ/B, UCL	Koller, P.C.	11	Y	Y
Academic	DoZ/B, UCL	Grüneberg, H.	9	Y	Y
Academic	DoZ/B, UCL	Philip, U.	3	Y	Y
Academic	DoZ/B, UCL	Gordon, C.	3	Y	Y
Academic	Bot. Dept., Kings Coll., Ldon	Catcheside, D.G.	8	Y	Y
Academic	Bot. Dept., King's Coll., Ldon	Gates, R.R.	2	Y	Y
Academic	Bot. Dept., Kings Coll., Ldon	Ramanujam, S.	2	N	N
Academic	Bot. Dept., Kings Coll., Ldon	Bhatia, G.S.	2	N	N
Academic	Dept. Zool., Aberdeen	Hogben, L.	7	Y	Y
Academic	Dept. Zool., Aberdeen	Gordon, C.	3	Y	Y
Academic	Bot. Dept., Manchester	Sansome, F.W.	5	Y	Y
Academic	Bot. Dept., Manchester	Sansome, E.R.	2	N	Y

Academic	Dept. Zoology, Liverpool	Bamber, R.	3	Y	Y
Academic	Dept. Zoology, Liverpool	Herdman, E.C.	2	N	N
Academic	Cambridge Uni.	Punnett, R.C.	8	Y	N
Academic	Bot. Sch., Camb. Uni.	Catcheside, D.G.	8	Y	Y
Academic	Dept. Bot., Uni. Glasgow	Catcheside, D.G.	8	Y	Y
Academic	Biochem. Lab., Camb. Uni.	Scott-Moncrieff, R.	5	N	N
Academic	Bot. Dept., Uni. Coll., Exeter	Richardson, M.M.	3	Y	Y
Academic	DoZ, UCL	White, M.J.D.	2	Y	Y
Academic	Eton College, Windsor	Morris, L.E.	2	Y	N
Academic	Dept. Zool., Oxford	Ford, E.B.	0	Y	Y
Medical	Dept. of Eugenics, UCL	Mather, K.	8	Y	Y
Medical	Dept. of Eugenics, UCL	Fisher, R.A.	2	Y	Y
Medical	Dept. Social Biol., Ldon Sch. Econ.	Hogben, L.	7	Y	Y
Medical	Royal Eastern Counties' Inst.	Penrose, L.S.	3	Y	Y
Medical	Burden Mental Res. Dept.	Fraser Roberts, J.A.	3	N	Y

### Appendix Four: British Geneticists 1910-1940

Setting	Location	Geneticists During 1910s	Geneticists During 1920s	Geneticists During 1930s
Breeding	Jl	Sutton, I.		
Breeding	Jl	Durham, F.M.		
Breeding	Jl	Bateson, W.	Bateson, W.	
Breeding	Jl	Pellew, C.	Pellew, C.	
Breeding	Jl	Richardson, C.W.	Richardson, C.W.	
Breeding	Jl		Newton, W.C.F.	
Breeding	Jl		Collins, E.J.	
Breeding	Jl		Chittenden, R.J.	
Breeding	Jl		Sverdrup, A.	
Breeding	Jl		Haldane, J.B.S.	Haldane, J.B.S.
Breeding	Jl		Darlington, C.D.	Darlington, C.D.
Breeding	Jl		Gairdner, A.E.	Gairdner, A.E.
Breeding	Jl		Crane, M.B.	Crane, M.B.
Breeding	Jl		Huskins, C.L.	Huskins, C.L.
Breeding	Jl		Andersson, I.	Andersson-Kottö, I.
Breeding	Jl			Mather, K.
Breeding	Jl			Lawrence, W.J.C.
Breeding	Jl			Philp, J.
Breeding	Jl			Upcott, M.
Breeding	Jl			Sansome, F.W.
Breeding	Jl			Scott-Moncrieff, R.
Breeding	Jl			Dark, S.O.S.
Breeding	Jl			De Winton, D.
Breeding	Jl			Lewis, D.
Breeding	Jl			Richardson,

				M.M.
Breeding	Jl			Brieger, F.G.
Breeding	Jl			Moffeff, A.A.
Breeding	Jl			Bartlett, M.S.
Breeding	Jl			Larter, L.N.H.
Breeding	Jl			Tseng, H.P.
Breeding	Jl			Fabergé, A.C.
Breeding	Jl			La Cour, L.
Breeding	Jl			Sutton, E.M.
Breeding	Jl			Thomas, P.T.
Breeding	Jl			Sansome, E.R.
Breeding	Jl			Stone, L.H.A.
Breeding	Jl			Afify, A.
Breeding	Kew Gardens	Hill, A.W.		
Breeding	Kew Gardens			Marsden- Jones, E.M.
Breeding	Kew Gardens			Turrill, W.B.
Breeding	S.E. Agr. Coll., Wye	Salmon, E.S.		
Breeding	S.E. Agr. Coll., Wye	Smith, G.		
Breeding	Amateur	Thomas, R.H.		
Breeding	Amateur	Caporn, A. St. Clair		
Breeding	Barley, Hertfordshire (Amateur)	Salaman, R.N.	Salaman, R.N.	
Breeding	Leceister (Amateur)	Bond, C.J.	Bond, C.J.	Bond, C.J.
Breeding	Amateur		Pitt, F.	
Breeding	Amateur		Lesley, J.W.	
Breeding	Sch. Agr., Camb.		Engledow, F.L.	
Breeding	Sch. Agr., Camb.		Watkins, A.E.	Watkins, A.E.
Breeding	Sch. Agr.,			Howard, H.

	Camb.			W.
Breeding	Sch. Agr., Camb.			Ellerton, S.
Breeding	Sch. Agr., Camb.			Morris, L.E.
Breeding	Animal Br. Res. Dept. / IAG		Crew, F.A.E.	Crew, F.A.E.
Breeding	Animal Br. Res. Dept. / IAG		Fraser Roberts, J.A.	Fraser Roberts, J.A.
Breeding	IAG			Koller, P.C.
Breeding	IAG			Lamy, R.
Breeding	IAG			Muller, H.J.
Breeding	IAG			Greenwood, A.W.
Breeding	IAG			Blyth, J.S.S.
Breeding	IAG			Bryden, W.
Breeding	IAG			Cochrane, F.
Breeding	IAG			Donald, H.P.
Breeding	Welsh Plt. Br. St.		Jenkin, T.J.	Jenkin, T.J.
Breeding	Welsh Plt. Br. St.			Williams, R.D.
Breeding	Welsh Plt. Br. St.			Silow, R.A.
Breeding	Welsh Plt. Br. St.			Ellison, W.
Breeding	Wisley Gardens		Buxton, B.H.	Buxton, B.H.
Breeding	Sch., Agr., Uni. Coll. North Wales		Fraser Roberts, J.A.	
Breeding	Sch. Agr., Uni. Coll. North Wales			White, R.G.
Breeding	Scottish Plt. Br. St.			Black, W.
Breeding	Scottish Plt. Br. St.			Gregor, J.W.
Breeding	Br. Res. Ass. Wool and Worsted Ind., Leeds			Fraser Roberts, J.A.
Breeding	Jealott's Hill Res. St., Bracknell,			Bartlett, M.S.

	Berks			
Breeding	Rothamsted			Fisher, R.A.
Academic	Cambridge Uni.	Doncaster, L.		
Academic	Cambridge Uni.	Bailey, P.G.		
Academic	Cambridge Uni.	Gregory, R.P.		
Academic	Cambridge Uni.	Wheldale, M.		
Academic	Cambridge Uni.	Doncaster, L.		
Academic	Cambridge Uni.	Fuchs, H.M.		
Academic	Cambridge Uni.	Cutler, D.W.		
Academic	Cambridge Uni.	Saunders, E.R.	Saunders, E.R.	
Academic	Cambridge Uni.	Onslow, H.	Onslow, H.	
Academic	Cambridge Uni.	Punnett, R.C.	Punnett, R.C.	Punnett, R.C.
Academic	Cambridge Uni.		Pease, M.S.	
Academic	Cambridge Uni.		Haldane, J.B.S.	
Academic	Cambridge Uni.			Catcheside, D.G.
Academic	Cambridge Uni.			Scott-Moncrieff, R.
Academic	Uni. of Reading	Keeble, F.		
Academic	Uni. of Reading	Jones, W.N.		
Academic	Uni. of Reading	Pellew, C.		
Academic	Oxford Uni.	Haldane, J.B.S.	Haldane, J.B.S.	
Academic	Oxford Uni.		Huxley, J.S.	
Academic	Oxford Uni.		Snow, R.	
Academic	Uni. of Ed.	Drinkwater, H.		
Academic	Uni. Coll. of S. Wales and Monmouthshire	Trow, A.H.		
Academic	Uni. Coll. of S. Wales and		Crow, W.B.	



	Monmouthshire			
Academic	Amateur	Harrison, J.W.H.		
Academic	Armstrong Coll.	Harrison, J.W.H.	Harrison, J.W.H.	
Academic	Imperial Coll.	Gates, R.R.		
Academic	Imperial Coll.	Dobell, C.		
Academic	Bedford Coll., Uni. of Ldon	Gates, R.R.		
Academic	Hazeleigh Rectory (Amateur)	Rayner, M.C.		
Academic	Amateur	Merritt Hawkes, O.A.		
Academic	King's Coll., Ldon	Gates, R.R.		Gates, R.R.
Academic	King's Coll., Ldon		Huxley, J.S.	
Academic	Kings Coll., Ldon			Catcheside, D.G.
Academic	Kings Coll., Ldon			Ramanujam, S.
Academic	Kings Coll., Ldon			Bhatia, G.S.
Academic	Dept. Zoology, Liverpool		Bamber, R.	Bamber, R.
Academic	Dept. Zoology, Liverpool		Herdman, E.C.	Herdman, E.C.
Academic	Dept. Zool., Trinity Coll., Dublin		Brambell, F.W.R.	
Academic	Leeds Uni.		Dry, F.W.	
Academic	UCL		Parkes, A.S.	
Academic	UCL			Haldane, J.B.S.
Academic	UCL			Koller, P.C.
Academic	UCL			Grüneberg, H.
Academic	UCL			Philip, U.
Academic	UCL			Gordon, C.
Academic	UCL			White, M.J.D.
Academic	Dept. Zool., Aberdeen			Hogben, L.

Academic	Dept. Zool., Aberdeen			Gordon, C.
Academic	Bot. Dept., Manchester			Sansome, F.W.
Academic	Bot. Dept., Manchester			Sansome, E.R.
Academic	Dept. Bot., Uni. Glasgow			Catcheside, D.G.
Academic	Bot. Dept., Uni. Coll., Exeter			Richardson, M.M.
Academic	Eton College, Windsor			Morris, L.E.
Medical	St. Thomas' Hosp.	Gates, R.R.		
Medical	Dept. of Eugenics, UCL			Mather, K.
Medical	Dept. of Eugenics, UCL			Fisher, R.A.
Medical	Dept. Social Biol., Ldon Sch. Econ.			Hogben, L.
Medical	Royal Eastern Counties' Inst.			Penrose, L.S.
Medical	Burden Mental Res. Dept.			Fraser Roberts, J.A.

## Glossary

**‘Setting’**: A group of locations with a shared purpose to their research. I identify three settings in this thesis: academic, medical, and breeding. These settings, and the term ‘locations’, are defined separately.

**‘Medical setting’**: The group of locations in which genetics was investigated, and where the research was intended to increase understanding of human pathology or human social deprivation and their remedy.

**‘Academic setting’**: The group of locations in which genetics was investigated, and where the research was intended to increase understanding of an academic discipline.

**‘Breeding setting’**: The group of locations in which genetics was investigated, and where the research was intended to aid agriculture, horticulture or animal fancying.

**‘Genetics Activities’**: A set of research projects performed for a shared purpose though not necessarily at the same location. In this thesis I distinguish between academic and breeding genetics activities. However, medical genetics activities also existed.

**‘Academic genetics activities’**: Genetics research that was intended to increase understanding of an academic discipline.

**‘Breeding genetics activities’**: Genetics research that was intended to aid agriculture, horticulture or animal fancying.

**‘Genetics Location’**: The geographic site where a cohesive group of geneticists or an individual geneticist performed research. For example, the Department of Zoology/Biometry, the Institute of Animal Genetics, the John Innes Horticultural Institution, the Eugenics Department at UCL.

**‘Hybrid Location’**: A location where the research was purposefully intended to fulfil more than one of the objectives which differentiate settings.

**‘Geneticist’**: Someone who published more than once in the *Journal of Genetics* in a given decade.

**‘Genetics’**: A body of theory relating to the structure, transmission, action and evolution of genes.

**‘Genetics Research’**: Any research that investigated genes, for whatever end and by whatever method.

**‘Type’ of genetics**: A configuration of defining characteristics.

**‘Defining characteristics’**: Types of a characteristic of science. In this dissertation I investigate three defining characteristics: types of funding body, types of research organism, and types of research problem. A configuration of these defining characteristics is termed a ‘type’ of genetics.

**‘Characteristic of science’**: A dimension of science, such as funding, research material, and research problems. A type of a characteristic of science is termed a ‘defining characteristic’.

**‘Programme of research’**: A series of research projects undertaken as a single enterprise, directed towards solving a scientific problem of wide significance. These are usually undertaken by a group of geneticists working as a research team at a single location.

**‘Research project’**: Research undertaken to solve one particular problem.

**‘Recurrent funding’**: Grants which were renewed periodically for the maintenance of a location in general.

**‘Project-focused grants’:** Soft-money received to do specific pieces of research.

**‘Soft money’:** Funding given to support research rather than a research location.

**‘Types of Organism’:** Groups of organisms that had either undergone design for the same features or, in the case of ‘wild organisms’, had not undergone design at all.

**‘Artificial organisms’:** Organisms whose genetic composition had been designed.

**‘Domesticated organisms’:** Organisms whose physical and/or behavioural characteristics had been designed.

**‘Wild animals’** Organisms that existed in the wild; whose genetic and physical characteristics had not been purposefully influenced by man.

**‘Physical model’:** An organism that is used as a model of a type group of organisms.

**‘Operational model’:** A model of an organism that, when deployed, allows researchers to treat organisms in particular ways.

**‘Holistic model’:** A model that portrayed research organisms as whole organisms.

**‘Gene model’:** A model that portrayed research organisms as sets of genes.

**‘Static model’:** A model that portrayed research organisms as unchanging.

**‘Dynamic model’:** A model that portrayed research organisms as changing and undergoing different processes.

**‘Homozygous model’**: A model that portrayed research organisms as having two identical alleles at each gene loci.

**‘Homogeneous model’**: A model that portrayed a group of research organisms as clones of each other.

**‘Problem choice’**: The specific question that motivated the research conducted.

**‘Research Area’**: A type group of questions, which form part of a science’s research ground. For example, transmission genetics, cytogenetics, developmental genetics.

**‘Research Topic’**: The particular abstract question that lies behind research problem. For example, the relationship between chiasmata and crossing-over lies behind the specific question of the relationship between the two in mice.

**‘Genetic Topics’**: Research topics that focused their investigation on genes.

**‘Cytological Topics’**: Research topics that focused on chromosome structure and/or behaviour.

**‘Cytogenetic Topics’**: Research topics that investigated both genes and chromosome structure/behaviour.

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