Tinbergian Practice, themes and variations: the field and laboratory methods and practice of the Animal Behaviour Research Group under Nikolaas Tinbergen at Oxford University.

Graeme Robert Beale

Ph.D. Thesis

The University of Edinburgh,

2008

I confirm that the content of this thesis is entirely my own work, and that all sources, quotations and pictures have been acknowledged and referenced.

(Graeme Beale)

26th April 2009.

Table of Contents

Acknowledgements

This thesis was made possible by an ESRC 1+3 grant, which covered both my masters and the Ph.D. research period. I was placed in the Science Studies Unit at Edinburgh University.

Graeme Beale, 05/04/09

An astonishing number of people need thanks for the help and support they have offered during the research and writing of this thesis. Firstly my supervisors: Steve Sturdy and John Henry, who have read more of my writing than may be good for their health. Their helpful comments, suggestions, supervisions and general support has undoubtedly got me through this thesis! I have had help too from the many current and former members of the SSU, including Carole Tansley, whose tea ceremonies became a requisite part of my day. My office mate, Donna Messner, was the perfect model of how to work as a Ph.D. Student. I have talked about my work to virtually all of the other members of the unit and many people also in ISSTI, including fellow students: Gethin Rees; Sian Beynon-Jones; Isabel Fletcher; Juan-Pablo Pardo-Guerra; Pablo Schyfter; and João Rangel de Almeida; and also staff, particularly Ivan Crozier. Their help, cheerful comments, and frequent scepticism towards my more outlandish ideas has been essential throughout this the research and preparation of thesis. Thanks also due to the computer guys – and yes five dead computers probably *is* enough.

Outside Edinburgh, Robert Hinde proved to be an interesting and informative interviewee, even though much of the material did not eventually end up in the thesis. The archivists at the University libraries of Cambridge, Harvard and Oxford all helped to make this thesis possible, and were friendly faces during my months travelling. Harvard University's Professor Allan Brandt also helped with access to those archives and in generally my time in Boston and Cambridge.

My parents and family have given more support and help than anyone would have a right to expect, and this thesis would not have been possible without them. Thanks also to my brother who has tried to interest me in birdwatching today, and even at managed to show me how it is done, including contemporary cliff-top bird studies. I remain the farrier who has never ridden the horse.

Finally and most importantly, this thesis is for my wife Yvonne, whom I love. She has been more supportive, helpful, and wonderful, than I could have thought

possible.

Abstract

This thesis investigates the work of Nikolaas (Niko) Tinbergen and his students, often known as the Tinbergians. Based on extensive archival research, and particularly on intensive study of fieldnotes – a resource largely untouched in previous historical enquiry – I throw new light on the scientific practices both of Tinbergen himself and the practices of individual students of his, including the relationship between research in the field and in the laboratory and the relationship between that research and the Tinbergians representation of their science, both to scientific and lay audiences.

Chapter one investigates Tinbergen's own background, and his writings on method and practice. This included a commitment to studying 'natural' behaviour, which led them to be wary of experimental methods that might distort such behaviour. Tinbergen's idea of the 'ethogram' – a complete listing of the behavioural repertoire of a species – is here linked to earlier interest in comparative anatomy as a means of elucidating evolutionary relationships Contrary to the work of Eileen Crist, who argues that ethologist concern to produce mechanomorphic descriptions of behaviour led them to see their animals as machines, I show that the fieldnotes regularly included anthropomorphic description, which only later was excised in writing up scientific publications where mechanistic description and a programmatic rejection of anthropomorphism were the norm.

The backgrounds of many of Tinbergen's contemporaries and students was considered in the first half of chapter two, and showed that almost all members of the school had a background in amateur natural history and strong personal and aesthetic affection for the animals they studied. The early fieldwork of the Tinbergians is examined in more detail in the second half of the chapter. This considers the work of two of Tinbergen's students: Robert Hinde and Martin Moynihan. Hinde's work is shown to be transitional between earlier approaches to animal behaviour and the more systematic methodology promoted by Tinbergen, while Moynihan's work instantiated a particularly pure expression of early Tinbergian ideals.

Tinbergen's Oxford laboratory is the subject of chapter three, looking in particular at how 'natural' behaviour was studied in an artificial environment. I look at the work of Desmond Morris, Margaret Bastock (later Manning) and J. Michael (Mike) Cullen. Morris's work reproduced field techniques of intensive close observation of behaviour in the laboratory. Bastock's work, largely overlooked by previous historians, showed interest in behaviour genetics. Cullen's work illustrates the difficulties of studying natural behaviour under laboratory conditions, and emphasises the value that Tinbergians placed on direct observation over other possible recording techniques. I then proceed to a more general consideration of the relationship between laboratory and field in the early years of the Tinbergen school.

Change over time is the theme of chapter four. Many of the early methodological commitments of the school were subsequently abandoned as the observation-led approach to behaviour gave way to a more explicitly theory-led and interventionist concern with causation, development, evolution and function. This was apparent both in the field and in the laboratory, and even included the occasional adoption of vivisection – a method dramatically at odds with the ethos of the early Tinbergen school.

The final chapter investigates how Tinbergen and others of his school communicated their work to amateur audiences, and shows that in some instances the anthropomorphic observations excluded for their scientific writings reappear in these more popular communications. I then link this to the Tinbergen school's long-standing interest in human behaviour.

The thesis is supplemented by a conclusion, and two appendices one listing the students studied in the thesis, and the other listing as many of Tinbergen's students as I can identify with surety.

Introduction to the thesis

How should we see the people who watch animals? That is the subject of this thesis. The study of animal behaviour in the mid twentieth century produced some of the liveliest scientific minds of the period, some of whom continue to contribute to both public and scientific debates today. The leading group of the period, both in terms of methodological influence and public profile was unquestionably the Tinbergen School of Niko Tinbergen at the University of Oxford. Tinbergen himself was a joint winner of the Nobel Prize for Physiology/Medicine along with Konrad Lorenz and Karl von Frisch, but his students have also achieved and in some cases surpassed him in terms of public profile. For this reason much of this thesis investigates the research of his students; both those who later became famous, such as Desmond Morris and Richard Dawkins, and also those who were important in the life of the group but did not achieve wider recognition, such as Margaret Bastock and Esther Cullen. In particular I will examine how each of these individuals practised their science, and how they interacted with the common features of Tinbergian practice, or being a Tinbergian scientist. This thesis is not an attempt at a classic Research School-study, in the tradition of J.B. Morrell (1972, 1993) and Gerald Geison (1978, 1993), instead it examines the work or works of a series individuals seeking commonalities, rather than assuming that all neatly or not so neatly form a unified group.

Tinbergen himself is at the heart of this thesis, but the youthful work of some of his students will also be introduced to the reader, particularly through investigating their D.Phil theses.[1] Tinbergen's own life story has now been reasonably well covered in the historiography, particularly by one of his own former students Hans Kruuk

1 There is anecdotal evidence that Tinbergen himself took a similar approach to teaching, preferring to use single exemplar documents studied in detail than through a broader approach, Tinbergen's former pupil Richard Dawkins for example reminisces:

> 'Nikos style as a tutor was unique. Instead of giving me a reading list with some sort of representative coverage of the subject, he would give a single, highly detailed piece of work, such as a DPhil thesis... I was asked simply to write an essay on anything that occurred to me as a result of reading the thesis or monograph'. (Dawkins, 1991:x-xi)

The style of this thesis then, could be seen almost as a homage to this approach. In fact it was more a reflection of the way that the documentary evidence fitted, but if as this little anecdote by Dawkins is correct this may partially explain why the documentary evidence is of a character that reads better as individual pieces then as fragments of a larger school.

(2003) and in his various autobiographical sketches (e.g. Tinbergen, 1954; 1985). At the level of the whole discipline of Ethology, it is hard to surpass Richard W. Burkhardt's Patterns of Behaviour (2005) which also covers both Tinbergen's individual work and that of a couple of his students, but in any such broad discipline–level study, there are figures whose work is sidelined or overlooked, and who therefore will be introduced to the historiography perhaps for the first time in this thesis.

This study will cover the period from Tinbergen's arrival in Britain in 1949 until his retirement in 1974. Before that time Tinbergen had been working in the Netherlands, and produced some of his most famous work there, including beginning his herring gull studies, and undertaking early studies of stickleback behaviour, both of which would become part of his most influential early book – The Study of Instinct (1951) – which was published soon after his arrival in Britain, but based on earlier research. This thesis aims to study the Oxford period, so his earlier Dutch work will not be included in a substantive way, though I will outline the early gull study in the introduction because it is referred to periodically throughout the introduction. This is not a study of "Tinbergen in Oxford" in the sense of how Tinbergen fits into the Oxford tradition of evolutionary and behavioural sciences, such as would fit with for example Kohn's (2004) exploration of the Oxford tradition of evolutionary and adaptational thought. Instead it investigates a series of particular instances of practice, for which the location was often Oxford, and undoubtedly in which evolutionary and adaptational thought played an increasing role, but in which evolution was only one theme, and Oxford not always the motor location

The introduction itself will be split into four sections, which deal with introducing Tinbergen himself, particularly his life prior to his arrival at Oxford, which is outwith the parameters of this study as a whole. This will also emphasise those of his pre–Oxford studies that will be referred to later in the thesis, particularly his red–spot tests on herring gull chicks and his early stickleback behaviour studies. The next section will deal with how I read the unpublished Tinbergian writing that formed the basis for most of this thesis. I will especially focus on Tinbergen's own fieldnotes, a

previously untouched historical resource. The notebooks will be particularly important as they represent my main route to exploring how Tinbergen was himself interacting with a way of being Tinbergian. This will be followed by a brief literature review of the history and historiography of the study of animal behaviour. Finally I will outline the thesis as a whole, and introduce the general arc of my arguments.

Section 1: Tinbergen, man, and animal observer

Tinbergen himself is an engaging historical character, a study in personal fortitude as well as being a scientist of considerable importance. His early life in the Netherlands was that of a childhood amateur naturalist and birdwatcher, as well as a talented athlete who played national field hockey (Kruuk 2003). Before the Second World War he participated in the International Polar Year, spending much of that time with his wife Lies living with the Greenland Inuit. He personally credited this experience with changing his outlook on animals, claiming that he learned to view them as Inuit hunters did rather than as sentimental Western Europeans did, and indeed would later describe himself as a hunter as much as a naturalist, even though for the bulk of his research he neither killed, nor dissected, nor vivisected the animals he studied.

This image of Tinbergen 'the hunter' was first observed by fellow Nobel prize winner Lorenz (see Burkhardt 2005:188) and has been much repeated (e.g. Kruuk, 2003: 52,62,68). Tinbergen was, as we shall see later in the thesis, a public opponent of anthropomorphic perspectives on animals, preferring to describe them as machines. Anthropomorphism, which means imputing human characteristics to animals, implies therefore at least a degree of empathy with them, if not a sentimental connection with them. Tinbergen was particularly tough on this sentimental approach, which had been exemplified in the work of someone like J.H. Fabre (1915) from the generation before. Instead he claimed that his understanding of animals came from this hunting perspective, and even that it was only because his ancestors had killed off all the game in Holland that he became a zoologist rather than a hunter at all:

> I am a zoologist. I have often wondered why I became a zoologist and now I think I know the answer. It is because in Holland I couldn't become a hunter (for that is what I really am, as Dr Lorenz has pointed out). Being a hunter at heart, I like to be in the open. I am perhaps also very lazy; I like to watch animals not to kill them. I have remained in the appetitive stage of hunting behaviour. I stalk animals and look at them.
>
> Later, when I compared myself with other zoologists, I discovered something else! As a boy, I liked to tease my brothers and my sister, to see what they would do when I interfered with them. Perhaps this led me to become an experimental zoologist. I like to find out what happens when you interfere, or interrupt an animal in its activities, or try to deceive it (Tinbergen, 1954:311).[2]

Tinbergen's time in the Netherlands was radically altered by the impact of World War Two, during which time he was interned by the Nazis for protesting against the removal of Jewish professors from Dutch universities (Kruuk 2003:115–128). After the war he took a post as Professor of Animal Behaviour at Leiden University, during which time he began studies on, amongst other species, herring gulls, particularly their chicks, and stickleback.

Section 1.1 Tinbergen's pre–Oxford Studies

Tinbergen's time at Leiden produced many studies, but two studies in particular stand out as being significant for his later work: those on herring gull chicks, and those on stickleback mating. His herring gull work sought to understand the mechanism which governed 'food–begging' in chicks, something he studied by removing the chicks from their nests and testing them with various two–dimensional cardboard models in order to determine which model generated the greatest response from the chicks. The models were initially of the heads of herring gulls with different coloured spots on their 'beaks'. Tinbergen tested the responses of chicks to see firstly which colour

2 The quote comes from an autobiographical sketch which the participants in the 1954 Macy Conference on Group Processes 1 were asked to provide.

garnered the most reactions, and whether having no coloured spot would have an effect; and secondly which shade relative to grey 'beaks' would garner the most reactions, in order to see the effects of contrast from the colour of the beak. Tinbergen measured responses by counting the times chicks pecked at the coloured spot, just as they peck at the coloured spot on herring gull beaks. He showed his results as here:

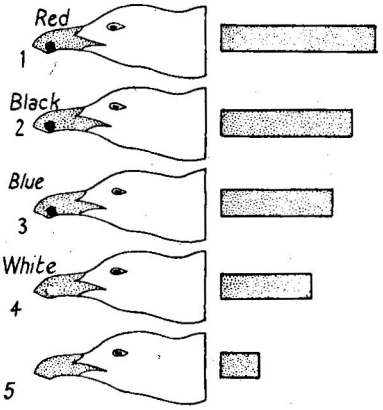


FIG. 22. Models of herring gull heads used to release begging responses in newly born chicks. Colour of the mandible patch varied (1–4) or absent (5). Columns indicate relative frequency of chicks' responses. After Tinbergen, 1949.

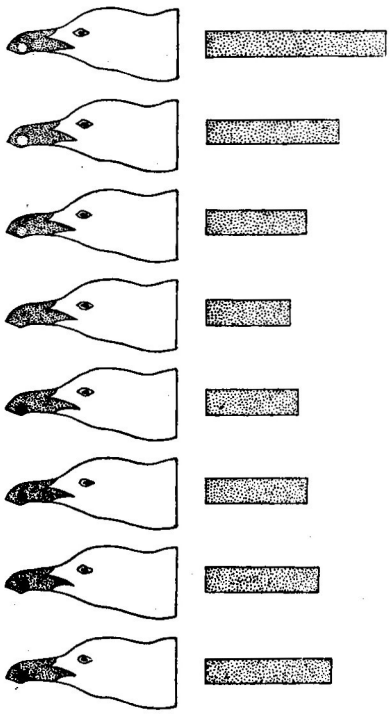


FIG. 23. Releasing value of herring gull models with grey bills with patches of varying shade. After Tinbergen, 1949.

(picture taken from The Study of Instinct, 1951:30 [image 1])[3]

As can be seen from the column on the left the coloured spot which gained the most attention was the red spot, the same colour as is on adult herring gull beaks, with other spots achieving less responses, and far fewer responses shown for no spot at

3 I have used Tinbergen's own reproduction of his original diagram from The Study of Instinct (1951). This was published soon after his arrival in Oxford, but based upon his earlier Dutch studies. I used Tinbergen's reproduction, because I could not find an original of the 1949 paper 'De functie van de rode vlek op de snavel van de zilvermeeuw (*Larus argentatus*)' in a good enough state of repair to scan the picture from with any clarity.

All further images significant images will have my image number in square brackets underneath them, because many of them have their own original "fig." number in the caption, but these numbers are not logically sequenced for the thesis.

all. The lack of a scale or any statistical data is very characteristic of Tinbergen and the majority of his students, who were more interested in recording observations and demonstrating them clearly both to scientific and public audiences, than in complex statistical manipulations. As a result this thesis does not discuss the small statistical side of the group's research. The column on the right of Tinbergen's diagram shows the results of Tinbergen's tests to see the significance of the degree of contrast between the spot and the beak as a whole. In these tests he tested spots in shades from black to white on a grey beak, and discovered that the greater the contrast of the spot from the beak as a whole the greater response from the chicks that was stimulated.

Tinbergen was interested in innate behaviour, and this was why he tested chicks, reasoning that as they were newly hatched they would not have been subject to great environmental or social pressures. He understood and described the behaviours he recorded on herring gull chicks as due to an 'innate releasing mechanism' or IRM, an idea that he had borrowed and adapted from Konrad Lorenz. IRMs (and in Lorenz's original phrase, innate perceptory mechanisms) were at the heart of the Tinbergians early work, and were an idea that was also strongly linked with Tinbergen's relationship with Konrad Lorenz. Lorenz suggested the idea of the releaser in his ground–breaking 1935 Kumpan papers, translated and abridged into English in 1937.[4] Lorenz's idea likened complicated behavioural responses to finding keys for specific locks, which then 'released' the behavioural mechanism:

> It is an old but fitting metaphor to liken the releasing set of stimuli to the key, and the innate perceptory pattern to the lock of the instinctive reaction. Even more appropriate, is the simile of a combination lock that cannot be opened except by a definite series of manipulations which, by reason of their general improbability, it is practically impossible to find by chance. The relation of the particular form of the lock to the key that fits it, or of any innate perceptory pattern

4 As Tinbergen both read and spoke fluent German, his contact was with the 1935 originals. Lorenz's original paper, especially after its translation, definitely impacted very strongly on the Anglo–American ornithological world, particularly after it influenced leading ornithologists including Margaret Morse Nice (e.g. 1941).

> to the set of stimuli to which it responds, is ever a compromise between greatest possible simplicity and greatest possible general improbability. The improbability of the innate perceptory pattern is to guard the instinctive reaction from being released by chance through other than the biologically 'right' influences. Surprisingly simple though the innate perceptory patterns are in the three cases cited as examples, they are evidently efficient enough, when natural conditions are taken for granted, to prevent the 'erroneous' unlocking of the reaction.[5] (Lorenz, 1937: 247–248)

Tinbergen was much taken with this idea of the IRM, particularly in this early pre–Oxford period, seeking to apply it to large number of behaviour studies on a wide range of species, from bee–wolves (a type of sand–nesting wasp) to sticklebacks, whose behaviour was studied in the laboratory. Lorenz's idea was ideal for Tinbergen, as it helped to provide a theoretical underpinning of his interest in innate behaviour. At this point, particularly American studies of animal behaviour were led by Behaviorists of the school of John B. Watson, who were principally interested in learned behaviour rather than any innate patterns, and who studied animals so that questions about human psychology might be better understood. Although Tinbergen too was interested in human questions, his studies of animals took place either in the field or in as natural a set of laboratory conditions as possible, in order to understand innate rather than learned behaviour patterns. Insofar as he sought answers to questions about humans, he did so only rarely, and usually by indirect routes, as we will see throughout this thesis.

Turning to Tinbergen's pre–Oxford laboratory, identification and understanding of IRMs was sought through experimentation. This artificial search for natural behaviour is a theme that will be particularly strong in chapter three of this thesis on the early laboratory in Oxford, but that work followed and directly referred to

5 Intriguingly Lorenz turned out to be incorrect about this idea that IRM's would be hard to release incorrectly, but in a way that was seen by Tinbergen as supporting the existence of the IRM: Tinbergen's discovery of 'supernomal' stimulators, for example in the red–spot tests, was seen as proof of the IRM. Here was an innate reaction that could be improved, even though the stimulator was profoundly unnatural– in this case a piece of wood with painted dots on.

Tinbergen's Dutch studies of three–spined sticklebacks, so it is worth outlining some of it here. Tinbergen tested the responses of stickleback males to a series of differently shaped and painted objects in order to determine the key releaser or releasers for aggressive behaviour. Tinbergen outlines the research:

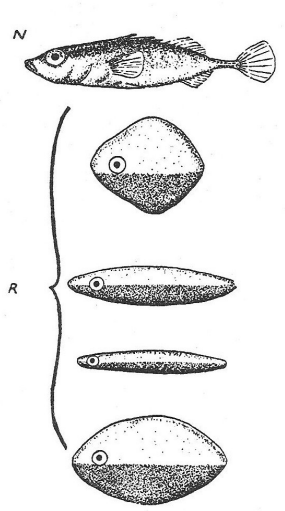


FIG. 40.—Models used in experiments on the release of fighting in male Three-spined Stickleback. A perfectly shaped silvery model (N) is rarely attacked, while crude models with red undersides (R) are strongly attacked (*after Tinbergen, 1951*)

> These stimuli have been analysed in various species by experiments and models. The male Three–spined Stickleback, while showing some hostility towards any trespassing fish, concentrates on males of its own species. Models of males release the same response, provided they are red underneath. A bright blue eye and a little bluish back add a little to the models effectiveness, but shape and size do not matter within very wide limits. A cigar–shaped model with just an eye and a red underside releases much more intensive attack than a (Fig. 40 [image 2]) perfectly shaped model or even a freshly killed Stickleback which is not red.
>
> Size has so little influence that all males which I observed even 'attacked' the red mail vans passing about a hundred yards away; that is to say they raised their dorsal spines and made frantic attempts to reach them, which was of course prevented by the glass wall of the aquarium. When a van passed the laboratory, where a row of twenty aquaria were situated along the large windows, all males dashed towards the window sides of their tanks and followed the van from one corner of their tank to the other. Because models of three times stickleback size although releasing a similar attack as long as they were not too close, were not actually attacked when brought into the territory, it seems that the angle subtended by the object is important and this must be why the distant mail vans were attacked. (Tinbergen, 1953a: 66–67)

Tinbergen's rather surreal vision of mail vans attacked by tanks of angry sticklebacks is what is particularly striking in the passage above. A sense of its enduring appeal can be found in the fact that it is still quoted in contemporary books on amateur natural history (e.g. Baker, 2004 :157). The study of innate or instinctive behaviour is what was being undertaken by Tinbergen here, even though the conditions and the stimuli were artificial. He was sure that the responses were natural, and had been 'released', thus demonstrating the power of the innate releasing mechanism by drawing attention to one of its 'mistakes'. These stickleback studies were much more comprehensive than has been suggested here, looking at the whole life–cycle of the three–spined stickleback. Indeed Tinbergen frequently stressed the importance of broad–based and long–term observation of behaviour, such that the observer was familiar with all aspects of a species' behaviour prior to any analysis. This was one reason for his noted opposition towards Behaviorism, which took single aspects of a species' behaviour and studied them intensively without having observed the full range of the behaviours of that species.[6]

Both his and his Oxford students' work in the laboratory and in the field will be extensively studied in this thesis, but both retained considerable continuities with the earlier Dutch period. The records for these Dutch observations are not nearly so good as for the later Oxford work, which is one reason why they are not the main subject for the thesis. Another is that the Oxford period in itself seems to be the most

6 Tinbergen later wrote what almost amounts to an ethologists' parable on the importance of general observation prior to experiment or analysis. He recounts the visit of a student from another university to his own ethological group:

> Since this broad observational approach is, in my opinion, of such extreme importance, I will elaborate it a little. I was once visited by a keen student from abroad who wanted to receive training in sociological work. He arrived with one very special problem in mind: he wanted to be trained in the technique of the experimental study of releasers. I tried in vain to convince him that he could better begin with a broad reconnaissance of a species; then let him have his way, and he started to count the number of bites aimed at a territory–owning male Three–spined Stickleback at a red model as compared with a silvery model. His results seemed to be variance with our previous work: the red models received only slightly more bites than the silver models. On doing the tests again it was found that the fish showed several signs of hostility other than actual bites (such as raising the dorsal spines, and making incipient attacks) and that these were released by the red models much more often that by the silver models. Having skipped the observational study of aggressive behaviour he had been unable to recognize and interpret these hostile movements. He then returned to just watching, and when, after some days, he resumed his tests, he got very clear–cut results. (Tinbergen, 1953a: 130).

interesting and the most productive of his life, in that his international reputation was cemented there, and his most famous, or perhaps infamous students emerge from this period. Of his students from his time in the Netherlands only G.P. Baerends achieved any great success, whereas his Oxford time was considerably more productive of great biological names.

Section 2: Notes on reading Tinbergen's fieldnotes

Tinbergen's published writings are both large in number, and in some cases quite well known historically; in the case of 'On Aims and Methods of Ethology' they are even still cited in contemporary science. However his fieldnotes have remained unexamined and for this reason I shall give a sense of the process of reading them in this section.

For both historical interest, and as a practical aid to the reader, I will set out some of the most common features of Tinbergen's fieldnotes. Since I will be reproducing several fieldnote pages at various points of this thesis, I will explain how to make sense of them. Each day's notes are different, because each day Tinbergen was observing different things, but there are many constant or at least regular features. To begin with, he always notes the day and the date at the top of the page. He then generally notes the location from which he is making his observation, and frequently mentions if he is observing with another person, or if he has discussed the observations with another person. After this point he normally writes down any behaviours he thinks are significant, and also theoretical or methodological questions which have been stimulated by these observations.

Stylistically there are several apparent features of the prose as well. Firstly the reader will see the constant abbreviation, which for Tinbergen takes many forms, such as using ♂ for male ♂♂ for a group of males. He uses the opposite characters ♀ and ♀♀ to denote individual and groups of females. He also abbreviates frequently used words, such as gull's full names, writing bl.h.gull for blackheaded gull for instance. Other common features include onomatopoeic description of the sounds made by the

birds he was watching, and also periodic unexplained switches from English into Dutch and or the other way around. Here is a short example of his fieldnotes and what they mean:

> Monday, May 21, 1951
> In hide at 2.40 pm to see tonight's tide (spring tide– see Martin's notes of yesterday.)
> I am 5 yds from the test bird of yesterday/ it was flooded last night and certainly today early, but is still sitting happily on 3 eggs.
> 2.43 relief at left nest sitter leaves just before partner arrives. No subsequent building.
> gull looks at nest rim, then picks up material and departs sideways and sure enough right after stands up and shifts.
> 3.33 again relief at left. Bird on nest koors and bends head down, newcomer kreeewws when approaching a light 3 yds from nest, collects material drops it there and preens, after some minutes flies to nest and relieves.
> 4– 4.06 ♀ is by nest [unreadable]
> is ♂. She approached softly keering, alighted 1 yr from nest. ♂ korred and built she korred and preened. Left at 4.06. ♂ goes to sleep.
> That this bird is ♂ is in line with his angry calling at a trespasser in the air which happened once. Nest relief comes at 4.15, when ♀ comes with nest material, calling keeworerr, keeoorr, drops it and low int. chokes – Three times she has to come with mat. before ♂ flies off. I should have good pictures. 4.25 bird on left nest calls and takes quietly off. My bird does not care and even does not look, its eyes are left half close. This shows very well how the way of taking off decides whether another bird will be alarmed or not. (Tinbergen, 1951, MS.Eng.e.2749)

This is not an exceptional passage from Tinbergen's fieldnotes, no great individual insight or analysis seems to be derivable from it, but for that reason it well serves the purpose of demonstrating an ordinary day's observations. It has many of the features

suggested above, including the noting of the date at the top, a series of observations recorded below peppered with the usual abbreviations, such as ♀ for female and int. for intensity. It also has a passage I have marked unreadable in square brackets which indicates, unsurprisingly, that the text is neither recognisably English or Dutch and may have degraded too much for any safe inferences about its content. This text also contains large numbers of onomatopoeic words, which describe the calls of the gulls they were studying; these include: 'koors', 'kreeewws', 'keeworerr', 'keering' and others besides. Finally it is quite clear that Tinbergen was timing these observations, with frequent noting of the time. He did not always note the time in his fieldnotes but noting these things was not unusual or out–of–character.

Overall Tinbergen's fieldnotes are not always easy to follow, but they repay the reader's time and energy in unexpected finds. Once the reading eye has become accustomed to his script, and fills in the many abbreviations, some of the pages can be read at near normal speed, thus creating a narrative of Tinbergen's private or semi–private view of his life in the field. Without them this thesis would have either not been possible, or would have missed much of the Tinbergians real practices in the field.

Section 3: Selected literature review

The study of animal behaviour in the mid twentieth century – sometimes called ethology – has been the subject of a moderate amount of secondary literature, both historical and sociological. Ethology has been studied by probably far fewer historical scholars than its nineteenth century antecedents, particularly Darwin's own work, and it has also attracted less sociological interest than one of its successor disciplines, Sociobiology.[7] In the literature which analyses ethology there are a large number of biographies and autobiographies, as well as some research which has tried to deal with the discipline as a whole.[8]

7 Though interestingly another successor discipline, one which Tinbergen himself showed some interest in – behavioural ecology – seems to have been almost entirely overlooked by historians and other science and technology studies researchers.

8 One area which I will not venture into is the debate surrounding Konrad Lorenz's Nazi past. Claims about Lorenz's Nazi sympathies began to be discussed around the time of Lorenz's book On Aggression (1966), reached a peak when he won the Nobel prize in 1973, and were

There are a few debates in the secondary literature which are extremely relevant to my research. I will begin by outlining the work of the doyen of historians of ethology, Richard W. Burkhardt's ideas of separate 'ecologies of ethology'. I will then investigate related questions from Robert Kohler's work on the importance of place and the relationship between laboratory and fieldwork for the development of biology – a very important consideration for the Tinbergians, whose work spanned field and laboratory. I will then explore the question of research schools, as in many ways Tinbergen and his students can be seen in such a context, and explain the rationale for my not choosing this as a principal means of investigation. Following this I will outline the debate over whether or not ethology was an anthropomorphic discipline, or whether its practitioners resorted to anthropomorphism, a debate that will be important in my thesis, and which is stimulated by the work of Eileen Crist, (1999) amongst others. Finally I will suggest how my research fits and contributes to these questions.

Section 3.1 Burkhardt and Ethology from Evolution to Ecologies

Richard W. Burkhardt, in a series of articles and books from 1981 to the present, has become the principal voice in the historical analysis of ethology. He began by arguing that the fundamental characteristic of ethology was that as a discipline it was a form of *Darwinian evolutionary thought*. His early work was concerned to trace the development of the discipline from Darwin's *The Expression of the Emotions in Man and Animals* (1872)[9] (Burkhardt, 1983a: 429–433, also 1983b), which even decades later influenced work on evolution and animal behaviour. After Darwin, Burkhardt argued, studies of animals had split into two strands: on the one hand there

subsequently renewed by Klopfer (1994) and Deichmann (1996). Lorenz's Nazism was conclusively demonstrated by Burkhardt (2005: 231–280), whose intensive archival work to this end was noted by Radick (2007). However as Tinbergen and his students are at the centre of this thesis Lorenz's status is not a central concern of mine, so it will not form a significant part of my investigations. In addition to the studies mentioned above Lorenz was studied by Kalikow (1975, 1976) and Richards (1974) during the time the Nazi controversy was at its height. In addition he has biographies by Nisbett (1976), and by R.I. Evans (1975) both written during his lifetime.

9 Darwin's *Expression of the Emotions* behavioural continuities between humans and animals, witnessed by the famous set of chimpanzee expressions and human facial expressions which are at the core of the book.

was interest in evolution from the comparative anatomists and physiologists, while on the other hand there were field naturalists interested in behaviour. However these two intellectual trends remained separate in post–Darwinian times until the work of Oskar Heinroth,[10] Konrad Lorenz (a student of Heinroth's) and Niko Tinbergen, in the decades either side of the Second World War.

From this early focus on evolution Burkhardt has shifted position, and in his mammoth *Patterns of Behaviour* (2005), he demonstrates a much wider understanding of the discipline based upon what he calls 'ethology's ecologies'. By turning to focus on these 'ecologies' he highlights the varied social, cultural and political as well as scientific arrangements that ethology both emerged in and also settled into, demonstrating that different contexts led to profoundly different ethologies. Burkhardt highlights the importance of each unique setting, both national and scientific, in the development of Ethology, citing these differences alongside differences of interest (whether theoretical or in particular species) as of great importance for the development of the discipline. His is a profoundly heterogeneous, locally situated view of ethology as a series of interrelated and interacting micro 'ethologies' created in response to local cultural, institutional or political circumstances and coloured by them, which could and did however still interact in 'distinctive and reinforcing ways' (Burkhardt 2005:474).

One context in which ethology emerged was highlighted by the Dutch historian D.R. Röell who suggested that the particular method of being *in* nature and *studying* nature (c.f. Röell, 2000: 87) was something that defined Tinbergen's ethology. 'Tinbergen did not begin his career with clearly defined questions about behaviour; these questions came later. He started out with a research method' (Röell, 2000:87).[11] In Röell's conc *Nederlanse Jeugdbond voor Natuurstudie,*[12] better known as the NJN (Röell, 2000:34–58). The NJN took children and young adults to observe nature across the Netherlands, and most of the cluster of early Dutch ethologists, including Tinbergen

10 Burkhardt has written a biographical sketch of Heinroth for the *Dictionary of Scientific Biography* (1990c).

11 Röell argues that Tinbergen himself saw methodology as the basis of Ethology: 'as far as Tinbergen was concerned, the development of Ethology was initially the development of a research method.' (Röell, 2000:87).

12 Dutch Youth Association for Nature Study (see Röell, 2000:44).

himself, Makkink, Kortlandt and G.P. Baerends, were all members of the NJN. Röell argues that the same kind of schoolboy interest in the study of nature that permeated the NJN can be seen in Tinbergen's push for his new science of Ethology to be the outdoor study of nature:

> His [Tinbergen's] ethological work in the 1930's grew out of his boyish love of outdoor activities combined with a special interest in natural history. This remained his basic motivation even in his later scientific work. (Röell, 2000:87)

Röell's work is persuasive inasmuch as it agrees with the common amateur background of many leading professional ethologists, a subject I will explore in chapter one. However, his work, as it focuses on the Dutch context, is again largely outside the scope of my study, which deals with the British context, and investigates the post–war work rather than the pre–war work. Furthermore, though it is potentially helpful in explaining the Tinbergen's own motivations, it would be naïve to apply it directly to every one of Tinbergen's students, as they were a varied group from many different countries of the world.

Section 3.2 Laboratory and Field

One larger theoretical question that affects this thesis is that of the relationship between laboratory and field in scientific endeavour. This is because Tinbergen himself and many of his students researched in both places, often trying to apply similar methods and practices. The relationship between the two arenas of scientific practice has been a central theme of much of science and technology studies, even interesting grand theorists like Bruno Latour (1999) in his study of Pasteur's laboratory as a lever to change the world around it. However the figures studied in this thesis operated under very different conditions to those investigated by Latour – the Tinbergians were was more focused on the field than on the laboratory, and had aims that were more observational than directly interventionist in the world as Pasteur's medico–veterinary laboratory had been. For my research, then, a much closer and more directly applicable set of ideas comes from work by Robert Kohler

in his Landscapes and Labscapes (2002).

Kohler's work, both on the history of the laboratory Drosophila (1993) and on the history of the relationship between field and laboratory (2002a; 2002b), argues that the mid twentieth century was characterised by the slow creation of border sciences between and across laboratory and field. This is particularly salient to my work, as Kohler suggests that fieldwork began to create new scientific spaces, unlike either the "pure" laboratory or the "pure" field. In building these new field sciences, the field biologists of this period, in Kohler's conception, recognised that there was a special place for unlablike practices which emerged directly from the conflict between trying to do scientific work in an uncontrolled space. He did state however, that this process cross border crossover did have limits, where the techniques of the laboratory could not always be applied in nature. (Kohler, 2002a:308)[13] This is something that Latour's laboratory centric view rather overlooks seeing the laboratory as the prime tool for changing the world. Kohler's work also suggests that there are challenges over applying methods or ideas developed in one place to the other, something that we will see as a theme throughout this thesis. Certainly these were challenges that Tinbergen and his students were aware of, though they chose to tackle them in quite surprising ways.

Kohler, in an earlier article, did suggest that field scientists operated in the 'borderlands' and were often treated differently to laboratory scientists, by those both within and beyond science. Beyond science, they were often mistaken for a large range of more or less reputable and characters, living and working on the borders of society.[14] This seems to have been true for the Tinbergians when they ventured

13 Kohler is quite clear that there are limits to this process of lab-field crossover, suggesting that at some point he sees an essential difference between the two locations of research, and therefore the research that is possible to undertake there:

> The differences between field and laboratory objectives, places, and practices still shape conventions still shape choices and careers in the border zone, because they are not mere conventions but facts of life. The line between nature and artifice can be blurred but not erased. Natural places cannot be made so lablike that they become unnatural; laboratories cannot be made so natural that they lose the artifice that gives them their power. So, too, with field and laboratory practices. Push quantification or modelling too hard and they become meaningless; take experiments too far afield and they are discredited. (Kohler, 2002a:308).

14 The full list of people that Kucklick and Kohler mention is: 'sportsmen, tourists, poachers, fish and game wardens, treasury agents, bandits, madmen, and colonial officials – in short, for just about

further abroad, but in Britain little more than polite confusions seem to have coloured the field. This may be due to the large amateur community with whom they interacted, but who in this instance by virtue of their size may have familiarised the public in Britain with the idea of the field 'naturalist' as a fixture of countryside life. Their working in such a public space though did mean that to a certain extent Tinbergen and his field students had to sacrifice the familiar prestige of the laboratory for a space which was still populated by amateurs, something that was not that case for many of his post–war laboratory–situated contemporaries. As a consequence of these problems, the constant negotiation between laboratory and field will be a major theme which structures much of this thesis – particularly chapters two, three and four.

Section 3.3 Research Schools and Ethology

The literature on research schools is both considerable and relevant in the case of ethology, the notion of a research school, first articulated by J.B. Morrell, (1972) in his comparative study of the research schools of Justus von Liebig at the University of Geissen and Thomas Thomson at the University of Glasgow. Since that period, the idea of the research school has been used extensively, particularly by Geison, who also edited a special volume of Osiris (1993) on the question.

Tinbergen and his students referred to themselves as the Animal Behaviour Research Group, however, in his time there, they achieved only partial official recognition, unlike for example the Edward Grey Institute for Field Ornithology,[15] (widely known as the EGI) which was founded by University Decree in 1938. Tinbergen's group also contrasts with Charles Elton's Bureau of Animal Populations which was given official university recognition alongside the EGI, when in 1947 the two were united

every sort of person known to have business (sometimes shady business) in places understood to be beyond the realms of civil society.' (Kucklick and Kohler, 1996: 10)

15 The Edward Grey Institute for Field Ornithology was founded in 1938, with W.B. Alexander as its director (Thorpe 1974:276). The EGI was a part of a movement that founded a series of institutions which had the effect of building a community of ornithologists, the two most important being the British Trust for Ornithology, (BTO) in 1933, following an appeal for money by a series of influential public figures including the then Prime Minister (see Fisher, 1953) its turn provided some of the funding for the Edward Grey Institute following its founding. Moss, the historian of ornithology argues that this period was overwhelmingly characterised by an impetus toward 'organised birdwatching' (Moss, 2004:128), and places the EGI in this context.

by university statute, to form the Department of Zoological Field Studies (Burkhardt, 2005:332). Tinbergen and his group never achieved the same level of official university recognition, and his appointment, as noted again by Burkhardt (ibid, 333) was to the Department of Zoology rather than that of field studies. Nevertheless on many factors Tinbergen's group can be seen as having some or indeed all of the characteristics of a research school and so I will outline what the constituent features of a research school may be.

Morrell (1972:3-7), before he begins his comparative study in detail, sets out a model for a successful research school. The main characteristics that Morrell identifies as being required to identify a research school as opposed to merely an individual or largely individual research enterprise are sixfold. Firstly a school needs a charismatic and influential director who can influence both the larger institution in which their school is situated, and also the scientific discipline in which they are interacting (ibid, 3). This ensures that the school can prosper institutionally, and also that the students in the school have the possibility of enhanced career prospects emerging from proximity to an influential director. Secondly a research school needs a defined programme of work, this serves to differentiate a school with a programme and a direction from merely the colleagues found in a research institution, for example, who may have largely unrelated research aims, and certainly no shared intellectual direction (ibid, 4). Thirdly any research school needs a steady supply of students to undertake the work and ensure the long term survival of the school (ibid). Fourthly a research school needs a unique set of techniques and practices specific to the school, all aimed at understanding a specific set of problems, which Morrell suggests helps to foster an *esprit de corps* (ibid, 5). Fifthly a school needs access to publication in order both that the findings can become widely known, and also that the students can establish their own reputations (ibid). Finally for any research school to function long enough to make an impact it must have access to stable sources of funding.

On five of these counts Tinbergen's group clearly can be seen as a research school, the only partial problem is in his relationship as a charismatic director, with the institution in which he was situated, as he was not put on an even level as the

directors of either the EGI or the Bureau of Animal Populations, and his research group did not achieve the same recognition in the university statute book. On the other questions Niko's group clearly can be understood as a research school in the sense that Morrell intended it to be used, as Tinbergen was himself a director with considerable influence over the science of ethology as a whole. In addition he had a firm idea of what work he wanted done by his students, specifically by describing the contributions to his 'gull work' (e.g. Tinbergen to Mayr May 15th 1958).[16] Tinbergen also had a constant stream of students to his research group, and in many cases these students were of the highest individual calibre, though he was ever concerned about ensuring continuing supplies of these students, a theme that will be explored in chapter five particularly. Tinbergen's students have a kinship in both techniques and in a close *esprit de corps*, however, as will become clear over the course of the thesis, there was considerable variance and variety in the place and manner in which these techniques were applied, with considerable change over time as well in the types of technique which were seen as permissible. Tinbergen's group had considerable access to publications, often from early on in their research stages, as he sat as a founder on the editorial board of Behaviour, in which many of his students published their work, again a topic that will be explored in chapter five. Sixthly Tinbergen had considerable success in securing funding, with an initial grant from the Agricultural Research Council, which was followed by a more considerable award from the Nuffield foundation that ran for a decade, and then by another by the Nature Conservancy with the express aim of creating a permanent field research unit (Burkhardt, 2004:337). Interestingly two further tendencies which Morrell noted of Liebig's chemistry school, though not of Thomson's considerably less successful Glasgow school can be seen to have echoes in Tinbergen's group. Liebig had to share quite cramped laboratory space with his students and so had very close contact with them, and close contact with his students was a characteristic of Tinbergen especially in the field, but also of his early students at the Oxford laboratory and at his own house. Secondly, Morrell describes Liebigs students having a form of 'disciple-fetishism' wishing to emphasise their close links with their teacher and mentor (Morrell, 1972:7), something which is also profoundly true of the students and

16 This is from a letter from the Mayr archive, HUG(FP) 14.17 Box "Correspondence with Konrad Lorenz and Niko Tinbergen." Folder 1955-9.

former students of Tinbergen, who often refer to him as 'the Maestro'.[17]

As far as Morrell's early model[18] is concerned therefore, the Animal Behaviour Research Group can be treated as a bona fide research school. Why am I choosing not to perform a classic research school study? Quite simply because there are more interesting questions about how some of the individual members of the school chose to work, and how they found different and changing ways of being Tinbergian. In this I include Tinbergen himself, whose public writings and pronouncements give a very clear impression of what working in a Tinbergian way entailed, something that he engaged with in quite different ways over the course of his career, and in ways that I think the reader will find quite surprising. Additionally, there has been considerable lack of clarity in the use and application of the term research school in connection with both Tinbergen and biological research in Oxford generally, which further dissuaded me from attempting this approach. This is because the term 'Oxford school' has been employed in the historiography by Marek Kohn (2004:contents page) in his work on 'Natural Selection and the English imagination' (2004:subtitle). [19] Kohn uses the term 'school' in connection with a range of zoologists including the geneticist E.B. Ford, the lepidopterist Bernard Kettlewell, and the head of the Edward Grey Institute for Field Ornithology David Lack; indeed he even mentions Tinbergen in this context, though it is unclear whether he considers him a part of this school. Amongst this disparate group there is little to show that they were interested or working on similar projects, using similar methods, or even in very close contact with each other. Indeed, if thinking of Morrell's categorisation of research school, this 'Oxford school' really does not stand up in any sense to any of his suggested tests. This further suggests that engaging in a school level analysis might not necessarily fruitfully elucidate the behaviour and practices of the Tinbergen school, and for this additional reason I shall avoid school level analysis and focus on the

17 As an example of just how pervasive this form 'disciple-fetishism' is in Tinbergen group comes from the cover of Hans Kruuk's (a student of Tinbergen) biography of Tinbergen; on which Richard Dawkins, another of Tinbergen's students calls Tinbergen 'the Maestro'.

18 Morrell later suggested that it was better to think of a research school more as a heuristic than as a real definable entity (Morrell, 1993). On either count though the Tinbergians seem to well fit this classification.

19 Kohn's book comes in for gentle criticism by John van Wyhe, (2005) as he points out that there is little empirical demonstration for Kohn's wider claim that there is a peculiar attraction between English or British Scientists and the idea of adaptation.

individuals themselves.

Section 3.4 Ethology and Anthropomorphism

One of the major themes of this thesis, which will particularly be a focus of the first and final chapters, is the relationship between ethology and anthropomorphism. Particularly there has been a focus on whether anthropomorphic thinking was built into the process of ethological research. Anthropomorphism in a simple definition is the attribution of human characteristics to non–human objects,[20] particularly animals (c.f. Mitchell, Thompson and Miles, 1997).[21] The process of anthropomorphising is one which was explicitly used by various students of animal behaviour such as E. S. Russell; however in general the leading ethologists including Lorenz (e.g. 1950) and Tinbergen (e.g. 1942) publicly wrote against it as a useful scientific concept.

Whilst they wrote against anthropomorphism, the work of many ethologists has been accused of anthropomorphic thinking by those outside the discipline. For example Kennedy (1992) argued that ethologists often write as though animals have either consciousness or interests. He analysed the idea of 'appetite behaviour', which is behaviour focused on accomplishing a particular task, such as 'nest–building'. He sees the ethological literature on nest–building, particularly that of W.H. Thorpe, as being absurdly 'goal–directed' (Kennedy, 1992: 36) i.e. that it leaves the reader with the impression that a bird is a sort of winged architect, building and repairing according to a consciously held plan or blue–print. Kennedy does not argue that ethologists are *intentionally* anthropomorphic, but instead views anthropomorphism as an *inherent* component of the practice of ethology.

Kennedy, a human psychologist, was writing very much in the vein of boundary–work, in Gieryn's (1983) classic phrase: seeking to 'defend' psychological categories

20 A large proportion of Mitchell, Thompson and Miles (1999) is focused purely on *defining* anthropomorphism, so my definition is certainly open to question. I sought only the broadest possible.

21 For a taste of the breadth of debates covered, Mitchell, Thompson and Miles includes essays: on the history of anthropomorphism (Knoll, 1992) and intentionality (Beer, 1992); amongst other headings. There are twenty–nine substantive articles in the book, by academics from vast range of disciplines, from biology, to psychology, to philosophy.

from application to animals, particularly in ways which implied intention. This kind of imputation of intention to animals he viewed as being inescapably anthropomorphic, implying furthermore that anthropomorphism was inherently *a bad thing* and must therefore be attacked at all costs.

The contrast with the sociologist and historian Eileen Crist's work (1996; 1998; 1999) could not have been stronger. Not only was she very sympathetic to the idea of anthropomorphism, particularly demonstrating how important it was for Darwin (e.g. 1872) and later natural historians like J.H. Fabre, but she also set out to demonstrate how anti–anthropomorphic the ethologists were. Indeed she compares the earlier natural historians' work with those of the Verstehen sociologists associated with Max Weber, calling this approach 'subjectivist'. By contrast, she described the writing of the ethologists as *mechanomorphic* (following Cenami–Spada, 1992), and argued that it sought to explain animals behaviour in the language of machines and mechanisms, leaving no place for intentionality.

The question of anthropomorphism will be an important one throughout this thesis. Though I certainly do not subscribe to Kennedy's reflexive antagonistic stance toward anthropomorphism, we will see that the picture is certainly more complex than Crist suggests with her assertion that ethology was essentially mechanomorphic.

Section 4: Outline of this Thesis

This thesis is structured in five main chapters, the first and fifth of which are generally thematic, whilst chapters two, three, and four are more broadly chronological. The thesis as a whole seeks to understand the field and laboratory practices of the Tinbergians, and how being each as individual researchers related to the shared challenges of observing and researching behaviour in animals, which occasionally included humans.

Chapter one looks first at the Tinbergen's background both personal and scientific, and then at the way that he chose to observe animals in the wild. In terms of my general argument this discussion of their way of observing is crucial, as it shows that

Tinbergen's fieldnotes tell a story that is much more complex than that of the published scientific work. In particular it shows that Tinbergen commonly used anthropomorphic language in the field, contrary to Tinbergen's methodological statements. This chapter will show that there *were* distinct elements of anthropomorphic thinking in the observations made by the Tinbergians.

In chapter two I examine in detail Tinbergen's statements on methods, and show two students' work, showing how closely they both followed his ideas in their fieldwork, particularly in trying to construct an 'ethogram' – a complete list of the behaviours of a species. Firstly Robert Hinde's work will be considered, followed by that of Martin Moynihan. Hinde's work is shown to have been informed many other influences besides those of Tinbergen; whilst Moynihan's is shown to be an exemplary early Tinbergian study, focussing especially on recording observations of behaviour in great detail, and in explaining those behaviours as stimulus–and–response patterns.

When we look at the laboratory, the focus of chapter three, I will suggest that its value in the work of the Tinbergians has been somewhat understated in previous historical writing, and that it played a more important role in the life and scientific output of the group than historians have previously suggested. The practices of laboratory workers will be considered in great detail, looking at the work of Desmond Morris, Margaret Bastock and Mike Cullen, and showing how Tinbergen's methods were applied in an area very different to the classic field studies.

Change is the theme of chapter four, as it tracks the development of Tinbergian research both in the field and in the laboratory. Both areas were subject to similar trends, though there were distinct differences also. In the field, evolutionary studies began to replace the old stimulus–response work, largely as a consequence of the research that Esther Cullen (one of Tinbergen's students) conducted on kittiwakes, which showed how adaptation–focused studies could be done in the field. Simple observation of behaviour became increasingly less common as there was a drift toward greater and greater intervention in the lives of the animals they were studying. This trend reached an apex in the laboratory studies of Richard Dawkins

and Juan Delius, when the intervention became intensive, and even in the latter case vivisectional.

Tinbergen's own and his students' public writings will be considered in the final chapter. This activity garnered Tinbergen and his students considerable fame, but it came at the price of periodic controversy. The Tinbergian way of observing animals, as I show in the early chapters always, contained an element of anthropomorphism, which helped them to see human behaviour as different only by degree of difficulty to comprehend. I will show that through much of his career Tinbergen was interested in applying his understanding of animal behaviour to explaining human behaviour also. Tinbergen's first attempt to develop this understanding at length, in a book manuscript entitled Man: Guinea Pig of Evolution (1974–5), ended in failure, the manuscript unfinished and unpublished. I will argue that this led Tinbergen to look for an opportunity to apply his observational methods more directly to humans, and that this was the impetus behind his studies of autistic children. The resulting book on autism in children observed an explained autistic children in surprisingly similar ways to those used to describe animals. In suggesting this I will be explicitly disagreeing with some of Kruuk's (2003) analysis of Tinbergen's autism work, in which he suggests that Tinbergen's later work failed to keep to the standard set by his earlier fieldwork. Instead I will suggest the picture is more complex. Much of Tinbergen's earlier work would not have met Kruuk's implied standards either, while the autism work was largely in keeping with Tinbergen's methodological practices. The autism work is a continuation of Tinbergen's earlier studies, in ways that previous historians have failed to acknowledge.

Chapter One: Tinbergen and the background to his Ethology

Introduction

Reading a current issue of *New Scientist* I was struck by an interview with the animal behaviourist George Schaller, introduced by the magazine as 'the greatest living field biologist'. It is always dangerous to view historical events with an overtly current eye, but one of Schaller's answers leapt out at me because it holds echoes of the ethos of the Tinbergians, showing just how strongly the general ideals of the Tinbergians still, even forty or fifty years later, hold field biologists in their sway. That approach, I will argue, was intimately tied up with affection for the animal subject, as Schaller suggests:

> How can you possibly sit for months and look at something you don't particularly like, that you see simply as an object? You're dealing with individual beings who have their own feelings, desires and fears. To understand them is very difficult and you cannot do it unless you try to have some emotional contact and intuition. Some scientists will say they are wholly objective, but I think that's impossible. Laboratory scientists wasted years putting rats in mazes to show they were learning. They never got close enough to a rat to realise that they were not going by sight and learning, they were following the scent trails of previous rats. By overlooking this simple fact they wasted years of science. (Bond, 2007:46)[22]

Schaller's outlook and his choice of illustration is resonant for me as a historian of ethology, because whether wittingly or no, it borrows directly from the criticisms made fifty years before by the Tinbergen and his students.[23] The 'rat maze

22 George Schaller was interviewed by Michael Bond for the *New Scientist* magazine 7th April, 2007.

23 To show just how closely Schaller's writing echoes that of the young Tinbergians, here is an excerpt from the autobiography of Desmond Morris, one of Tinbergen's most publicly known students. Note in particular the way that Tinbergians viewed how behaviourists studied their test subjects:
Animal psychologists came in for a great deal of harsh criticism on this score. How could a man

psychologists', so often the Tinbergians shorthand for the Behaviorist school of John B. Watson and B.F. Skinner, represented everything that was wrong with the study of animal behaviour; clearly for Tinbergen's heirs they continue to do so. Behaviorists focused on learned or conditioned behaviour rather than the natural behaviour or instinctive behaviour studied by the Tinbergians; Behaviorists studied their animals under the most controlled laboratory conditions possible, where Tinbergians sought out windswept sand dunes, perilous cliffs, and blasted heaths to watch their animals in the wild; Behaviorists saw their animals as individual units of scientific study, Tinbergians as actors in great trans–species social dramas. This at least was how biologists injected with the Tinbergian ethos understood it, even if not all aspects of these dichotomies were as simple as I have suggested here.

Tinbergen described his approach as 'objectivistic' (Tinbergen, 1942: title) by which he meant three distinct pillars: firstly that ethology had to be based on *directly observable phenomena*;[24] secondly that ethology should avoid anthropomorphism, by which he means it should *never explains animal behaviour as the consequence of concious or semi–concious motive;*[25] thirdly he argued that ethologists should *not seek to understand the internal mental state* (the subjective life) of the animal under study.[26] These three ideals necessarily entail a great deal of overlap, and it is rarely

study a white rat when he had never seen it make a burrow, for instance? The burrow was the very centre, the core of the rat's existence. And how many hundreds of 'rat psychologists' had provided burrowing facilities for their animals, and watched them at work constructing their natural home base? The answer was simple: none. So much for psychologists who claimed to study animal behaviour. As budding ethologists we had no time for them. (Morris, 1979:76)

24 He states this is what he means by objectivist in a lecture given to his students, which is sadly undated, and also in a guest lecture given at Seattle. (Tinbergen: n.d. MS.Eng.c.3131/c10 'Final Lecture:Evolution of Behavior'; n.d. MS.Eng.c3131/c14 'Seattle Lecture'.)

25 This is also stated in the same lecture on the evolution of behaviour (Tinbergen: n.d. MS.Eng.c.3131/c10 'Final Lecture:Evolution of Behavior').

26 In stating this Tinbergen was at his clearest. He takes the example of hunger – and in the passage that follows is directly writing to counter the ideas of Bierens de Haan:

> ...Because subjective phenomena cannot be observed objectively in animal, it is idle either to claim or to deny their existence. Moreover to ascribe a causal function to something that is not objectively observable often leads to false conclusions. It is especially dangerous in that the acceptance of the conclusion kills our urge for continued research.
>
> To mention an instance: the conclusion that an animal hunts because it is hungry will satisfy many people at first glance. Yet the use of the word 'because' is ambiguous, since 'hungry' may be used as (I) a *convenient description* of the state of the animal, based on subjective as well as objective criteria. When the word is applied in this way, the conclusion will be clearly seen to be a very provisional one and will not satisfy the scientist who wants to know what is happening inside the animal when it is in this state. He will try to find out what impulses come from, and so on. But when the conclusion that the animal hunts because it is hungry is taken literally, as (2) a *causal explanation,* and when it is claimed that the subjective phenomenon of hunger is one of the causes

clear either in Tinbergen's own work, or in the long debates since, which particular facet is being addressed at any one time. For example to explain an action as a the consequence of an internal mental state necessarily infers some understanding of what that state might be – one may explain an action as the consequence of nervousness, but in order to do that one has already assessed the mental state as being that of nervousness.

However, although he made both public and scientific statements to this effect, which I will examine in Section 2. I will also show that his field practices made a great deal of use of anthropomorphism, and in some ways required a level of anthropomorphic reasoning in order to make sense of their observations. As a consequence of these stated beliefs about objectivism and subjectivism in his scientific writing he built deliberately objectivist accounts of the animals he studied. What makes his work so interesting to me however is that after reading his fieldnotes I became certain that there was more to this observer than was always revealed in his scientific writing, and this has been overlooked by previous work on the school. Partly, I feel this is because they took his pronouncements at face value, and partly because he has become such an icon of the objective study of behaviour, an image that he worked hard to foster.

Tinbergen, then, successfully cast himself, through his writing, as the leading proponent of the objective study of animal behaviour, which is sustained by the three pillars I outlined above. I will give a sense of how strongly he has become associated with this approach with a volume of evidence from various different academic approaches. As a first example of this view of Tinbergen I will present a brief quotation from Eileen Crist's work:

> Nikolaas Tinbergen’s depiction of gulls illustrates how displays can be portrayed in a manner that extinguishes their apperception as gestures. The invocation of human experience and use of lyrical language are all

of food–seeking behaviour, physiological and psychological thinking are confused. Although, as we said before the ethologist does not want to deny the possible existence of subjective phenomena in animals, he claims that it is futile to present them as causes, since they cannot be observed by scientific methods. (Tinbergen, 1951:4–5 italics in original).

but completely absent in Tinbergen's work on gulls. (Crist, 1999:180).

Other historians have also emphasised Tinbergen as profoundly anti–anthropomorphic, in the sense that he bracketed off questions of an animal's subjective experience, and that he would not accept subjective explanations for a specific animal behaviour. Kruuk for example, states: 'Right from the beginning the scientist in Niko felt uncomfortable with the subjectivity of both method and conclusions' (Kruuk, 2003:76). This passage comes amidst a discussion of the work of Fritz Portielje, one of Tinbergen's forbears in the Dutch naturalist community. Portielje was interested both in the behaviour of birds, and also the subjective experiences that the birds had; it is this which, in Kruuk's rather stilted phrase, Tinbergen chose to reject, when he was rejecting subjectivity in method and conclusions.[27] Kruuk makes an explicit link between Tinbergen's objectivism and his mechanistic approaches to behaviour analysis. Kruuk links this objectivism with Tinbergen's visit to Greenland, and a year Tinbergen spent with the Greenland Inuit suggesting that his time there, particularly that spent hunting with Karale[28] led him to a much more mechanistic and less sentimental view of animal behaviour, than would other wise have been the case. Kruuk therefore ascribes Tinbergen's view of animals as 'behaviour machines' as being directly attributable to his time in the arctic. (Kruuk, 2003:69).

A sense of the extent to which the image of Tinbergen as the arch anti–subjectivist has permeated the academic sphere can be seen from a variety of further sources. The philosopher Bernard Rollin, for example, mentions anti–subjectivism as being perhaps the only thing shared by mid 20th century Behaviorists on the one hand, and

27 It should be noted that at this time there were both Dutch and British proponents of subjectivist studies of animal behaviour. Alongside Portielje, there was Bierens de Haan, the leading Dutch animal behaviorist of the period, and in Britain E.S. Russell was amongst the leading students of animal behaviour. Kruuk was a product of the Tinbergians, and also of the era that followed in which subjectivist approaches to animal behaviour were largely ignored or left far from the mainstream, for which Tinbergen's public and scientific work formed crucial intellectual ballast. I note this because I think it is significant that Kruuk calls it the 'scientist' in Tinbergen that rejected subjectivism, where in the period itself subjectivist answers to questions of animal behaviour were perfectly scientifically acceptable. Kruuk's use of the word scientist, is a classic example then of the Whig view of scientific history, in which today's approach is lauded as the correct one, and all movements towards it are seen as steps in the 'correct' direction.

28 Karale was a Greenlander whom Kruuk mentions that Tinbergen was living with and learning from (Kruuk, 2003:62).

Lorenz and Tinbergen on the the other. (Rollin, 2000:109). Burkhardt, making his own criticisms of Eileen Crist, disagrees that it was their use of mechanomorphic language that made them anti–subjectivist (a key claim made by Crist), arguing instead that it was a long–standing objection to subjectivism that made them emphasise objectivism. Indeed he is quite critical of the idea that it is the language of mechanomorphism which imprisoned the Tinbergians in a mechanomorphic thought process, arguing that this denied them the agency to think for themselves. Instead he argues that this was a conscious choice of Tinbergen himself to move away from subjectivist approaches toward objectivism:

> Certainly, by the late 1930s and early 1940s, he was committed to "desubjectifying" the science of animal behavior. He contrasted his "objectivistic" science of ethology to the approach of his countryman, the animal psychologist J. A. Bierens de Haan, who believed that the subjective experience of animals was necessarily animal psychology's primary concern. (Burkhardt, 2000:391–392.)

Burkhardt's analysis suggests that Tinbergen felt his field depended on maintaining an objective approach to the study of animal behaviour, and separately, that it bracketed off questions of animal subjectivity. This quotation then contains another example of Tinbergen being understood as the arch anti–subjectivist, and the leading proponent of objectivist studies of animal behaviour.

My final example of the classic portrayal of Tinbergen as a leading anti–subjectivist in both theory and practice comes from Bekoff's work on animal mind, in which he is notably accommodating to the notion of studying animals' subjective experiences. Bekoff, a contemporary philosopher and psychologist, in spite of his relatively positive view of the possibilities for the study of animal subjectivity, still sees Tinbergen as representing the arch opponent of the possibilities for studying animal subjective experience, and the use of subjectivist approaches to answer questions about animal behaviour:

> Niko Tinbergen is often called "the curious naturalist."[29] Tinbergen worked with Lorenz on a number of classical problems including egg rolling that was performed by geese of different species. Once the egg–rolling began, it continued even if the egg was removed from under the mother's beak. Tinbergen and Lorenz showed that geese would choose to retrieve eggs that were orders of magnitude larger than their natural eggs; they called these eggs "supernormal" stimuli.
>
> Tinbergen was a skilled and dedicated field biologist who studied a wide variety of behavior patterns ranging from homing in wasps to antipredatory behavior in birds. He stressed that in studies of behavior we need to pay attention to the evolution of the behavior, what caused it, how it helped animals adapt to their environments, and how it developed. Ethology was truly an integrative science. Tinbergen was an eclectic biologist. Later in his life he and his wife studied human autism, applying ethological methods to learn about this disorder. Perhaps surprisingly, he refused to study the emotional lives or subjective states of animals because he believed we could never learn much about them. (Bekoff, 2002: 37)

The key line here is the very last, where Bekoff absolutely accepts the claim that Tinbergen refused to study the emotional lives or subjective states of animals. This, in combination with the many examples I have shown above, demonstrates just how effective Tinbergen had been at persuading the scientific and lay community that the way to study animal behaviour was objectivist, and this was the way that he had done it. Having given evidence of how pervasive is the view of Tinbergen as the arch anti–subjectivist, and as someone who always maintained objective distance from his subjects of study, my challenge for this chapter will be to change this perception. In order to do this I will outline where Tinbergen and his fellow ethologists came from, how in practice they behaved in the field, and how they wrote about animal

29 Actually, having read a great deal about Niko Tinbergen, except for in his own book Curious Naturalists, (1958 & 1974) there are almost no references by other people to Tinbergen as "the curious naturalist," during his lifetime. However since his death, and particularly with the restimulation of interest in his work that has followed Kruuk's Niko's Nature (2003) and Burkhardt's Patterns of Behavior (2005) this phrase seems to have frequently surfaced.

behaviour in their fieldnotes.

This chapter therefore will be split into three segments; firstly I will look at the Tinbergen's own background, where he as an individual came from, and how this affected his approach to the animals he studied. I will emphasise their time as field students of Tinbergen's but also the common background of so many field biologists in amateur naturalism or ornithology, both of which carry with them the amateur's love of nature and for the latter specifically birds. The second segment, in order to examine Tinbergen's field observations will investigate the importance of seeing the world from the animal's point of view. The third part of this chapter will be focused on the importance of seeing bird life as *social drama*, an idea that flows easily from attempting to see the birds' point of view. This approach however came with the corollary of beginning to talk about and see individual named birds as social actors in dramas played out on canvasses that describe birds as 'Cleopatra' and 'Casanova,' who are of course cultural touchstones for specific dramatic personae. This should all serve to introduce the Tinbergians way of working, and particularly their manner of observation.

Section 1: Tinbergen's Route to Ethology

Tinbergen did not arrive in scientific ethology entirely untutored in the ways of the field, indeed in ways that Röell (2000) in particular demonstrates that Tinbergen's interest and affection for the fieldwork approach to animal behaviour study was a common feature of many of the Dutch ethologists. However one feature in particular will be the focus of this section, Tinbergen's understanding of the birds he was observing, which followed closely on the aesthetic appreciation that he felt for them. My argument in this section runs counter to that of Eileen Crist, in her elegant study of the idea of anthropomorphism in studies of animal behaviour since Darwin, who argues that what is characteristic of classical ethologists such as Tinbergen is a distance and mechanomorphic description of their animal subjects, which she contrasts to earlier 'naturalists' such as Fabre or Darwin who were comfortable with

direct anthropomorphism. Writing on Darwin she argues that he deliberately used anthropomorphic descriptions of animals to lessen the distance between descriptions of animals and those of man, to demonstrate homology and further the case for evolution (Crist, 1999:49). She contrasts the approaches of Darwin and other 'naturalists and protoethologists' to Tinbergen's in their writing on birds:

> In comparison to the early naturalists, it is also evident that there is a marked shift in what motivates the study of animal behavior for ethologists. With naturalists, or "protoethologists," there is a desire to understand animal life directly, to grasp the meaning and feeling of action from an experiential perspective. With Lorenz and Tinbergen, preoccupations become far more intensely theoretical, overshadowing a concern with an immanent perspective and eliding to a large extent the visual, phenomenological icon of behavioral events. (Crist, 1999:93).

My studies of Tinbergen's life and field practices in particular do not support Crist's interpretation, because although the published work of both Tinbergen and Lorenz does seem to fit this picture, when we look at the fieldnotes and the associated fieldwork Tinbergen is clearly behaving in a different way to that suggested by his academic writing.

Burkhardt in his review of Crist's work, disputes Crist's hard categorisation of animal behaviour researchers into discrete groups which she labels as ethologists, sociobiologists and naturalists. Instead he suggests that this categorisation would not have been meaningful as many ethologists saw themselves as 'naturalists', and were comfortable with that label (Burkhardt, 2000:391).[30] There is no obligation on the historian to slavishly follow the categories of the period they study, but nevertheless the fact that there was not felt to be a hard categorical division at the time is damaging to Crist's idea because it suggests that these different groups may have felt

30 Burkhardt's critique in full is:

> Still, at least a couple of issues do arise. One stems from the fact that Crist's typology of naturalists, ethologists, and sociobiologists does not necessarily sort her actors out in ways that would have seemed most meaningful to them. Tinbergen, for example, was unquestionably an ethologist, but he at the same time self–consciously identified himself as a naturalist. (Burkhardt, 2000:391).

stronger kinship in their motivations to study their animals than Crist acknowledges. For example, Tinbergen was concerned to position himself as an objectivist who made careful theoretical observations of species, but he retained a strong link with amateur naturalism, because he, like so many ethologists, had emerged from this tradition. The second reason for not accepting Crist's assertion that field ethologists had very different motivations from their naturalist predecessors is that the evidence from the fieldnotes is quite different, as these too show an aesthetic as well as a theoretical appreciation of their subject, something that I will bring out over the course of this chapter.

I will demonstrate that far from being the distant mechanistic observer suggested by Crist, rather there was strong affection felt by Tinbergen for his animal subjects of study and this affection is evident in his field studies, and as will become clear in chapter two this affection certainly can be found in many other ethologists, and amongst early students of Tinbergen.. For example Tinbergen's most famous studies were on gulls and his affection for gulls pre–dates his biological study of them as he himself states:

> Throughout the years of my boyhood watching the life in the large gullery was complete happiness; and I derived a vague but intense satisfaction from just being with the gulls, feeling the sun upon my skin, enjoying the scents of the lovely dune flowers, watching the snow–white birds soaring high up in the blue sky, and assuming, or rather knowing, that they were feeling just as happy as I was. (Tinbergen, 1953b:xiii)

Tinbergen's infectious sense of the joy of ornithology is something that is clear throughout his working life. This he seemed to carry with him, in spite of, or perhaps even because of the lack of comfort and domestic luxuries that fieldwork at that time implied. Morris, in his recollection of first meeting Tinbergen notes that it was Tinbergen who sat on a wooden crate, whilst Morris, the student, was offered the fine chair in Tinbergen's Oxford college rooms. Morris suggests the overall impression was 'as if Niko were only camping in civilisation, before returning to his true home

in the wild' (Morris, 2006:71). Indeed this love of field life shines through Tinbergen's cheerful descriptions of the conditions that they lived in through this extended fieldwork period:

> Life on the islands was delightfully uncomplicated. We often got up just when the very first glow of light appeared on the eastern sky, had a cup of coffee and a slice of bread and then set out for the cliff. Mike Cullen, whose terns did not arrive until the beginning of May, spent the first two months of each season watching Shags.
>
> Observing the birds on the cliff was cold work. Although it was rarely freezing, even temperatures of 40 degrees can make one quite miserable when they go with clouded, windy and wet weather. The first hour would not be bad, but then the cold began to creep in slowly but steadily; and there was nothing you could do against it, for bird watching of this kind just means sitting still. We were armed with heavy clothing: layer upon layer of wool, with duffelcoats on top, covered again by windproof coats. In order to keep our hands warm enough for fast writing, we had heavy fur–lined gloves, yet at the end of four hours' watching none of our joints could move as it ought to. (Tinbergen, 1958:193–4)

The uncomfortable conditions of Tinbergen's fieldwork went hand in glove with the affection that he had for the birds. Indeed that Tinbergen frequently refers to 'my bird' in his fieldnotes, suggests that he felt some sense of ownership or responsibility toward the birds he was studying. That aesthetic motivations may have partially underlain the desire to be out and amongst the birds should not be of surprise to someone of a Strong Programme background,[31] in which interests, including aesthetic and emotional, are understood as having profound influence over the scientific outcomes of experiments, or even, as is the case here, research schools. Clearly stated, I believe the evidence I have shown above demonstrates that Tinbergen was not a disinterested observer, whose primary reason for studying animals in the wild was to answer specific theoretical questions, as Crist suggested at

31 I am referring here to the Strong Programme in Science and Technology Studies.

the beginning of this section. Rather, I argue, he was in part motivated because he derived pleasure from merely being with the birds and observing them, and had done this as an amateur before he became a scientific professional. This prior amateur, and even childhood interest had profound effects for ethology however in that there was an extremely strong reluctance to cause hurt or harm to the birds he was studying, something which pushed his studies towards whole animal live studies in the wild, in which minimal harm could be caused to the animal. The antithesis of this would be some kind of highly interventionist study in which surgery or mutilation was involved, and which the early ethologists tended to avoid, choosing observational studies instead.

Section 2: Dissecting the field, Tinbergen's ideas of field methods

Tinbergen with his binoculars hung around his neck is perhaps the archetype of the modern naturalist and observer, indeed he even titled his own autobiography 'Watching and Wondering' (Tinbergen, 1985). Having read both Tinbergen's published writing on his field practices, and also his fieldnotes I will outline the complex web of theory and practice that was Tinbergian fieldwork, with a particular focus on the relationship between observations and their analyses. Tinbergen was noted as an experimenter,[32] but it is his and his students' approaches to observation and analysis which are I think the most interesting and under–analysed area of his research,[33] and which will therefore follow as the central theme of this chapter. There

32It has been repeated to the point of cliché that he devised 'ingenious experiments', an idea dating from the very early reviews of The Study of Instinct, (1951), for by example Aronson (1953:69); but continued right up to the Nobel Presentation Speech to him, Lorenz and von Frisch (Cronholm, 1973). Lester R. Aronson was an American student of behaviour, but working on the laboratory analysable physiological aspects. It is noteworthy, I feel, that his review was actually quite critical of Tinbergen's approach, and his focus on innate behaviour. This particularly well illustrates the gulf between the animal physiologists and the ethologists. Aronson made his name on a series of studies of amphibian sexual behaviour, by, for example inducing sexual arousal by injecting pituitaries: see for example, Kingsley Noble and Aronson (1942).

33 For example Kruuk (2003) foregrounds Tinbergen's experiments, from the very earliest pre–war period of interaction with Konrad Lorenz through to Kruuk's own time with Tinbergen in the 1960s. This should perhaps be unsurprising given Kruuk's own situation, but it can lead us to overlook the area of observation and analysis, where Tinbergen's school was more distinctive. Crist (1999: 106–116) also foregrounds Tinbergen's experimental work, which is odd as he himself wrote that

are a range of key objects of Tinbergian methods which need explaining, and they will form the subsections of this chapter. Firstly I will look at Tinbergen's own writing on methods, secondly I will explain the importance of the heritage of comparative morphology for Tinbergen, and thirdly I will examine the importance of the idea of the ethogram for Tinbergen and his students.

Section 2.1 Tinbergen's Writing on Method

Some features of Tinbergen's methods were common to many of his students, as we will explore in later chapters, such as lengthy periods of observation prior to any analysis, or an insistence on studying the animals being observed under as near natural conditions as possible, and the reasons for this can be found in Tinbergen's own writing on methods. The Tinbergians tended to begin any analysis only after a long period of observation, although this standard was not always achieved as will be shown below. There was considerable variation in the nature of the analysis that followed the observations, most prominently in the level of intervention in the lives of the animals under study. There are hints throughout the primary and secondary literature that the methods of the Tinbergians in their early period were at least partially recognised as being something different or unusual. Kruuk, for example is in places very critical of the standard of experiments and their analysis done in the field, linked those experiments that occurred in the field with the nature of the observations made there: `Ian Patterson remarked that Niko's 'untidiness with experiments' was probably largely due to his quickly seeing from the animals' behaviour what was going on, then collecting data just to substantiate that.' [34] (Kruuk, 2003:216)

The comments made by Kruuk's interviewee and fellow student of Tinbergen, Ian

experiment should only follow extended observation and analysis. Burkhardt's work (2005) focuses more on the theoretical and institutional history than on the way that observations were made, as his aim is to trace the links between the theory and the different settings that ethology flourished in. Röell (2000) did mention that observation was essential for ethology, however this was almost completely at the expense of considering any of Tinbergen's experimental interventions in the lives of his subject animals, a point made by Dehue (1997). Dehue was reviewing the original Dutch book rather than its 2000 translation into English.

34 Kruuk is quoting from an interview with Ian Patterson, one of Tinbergen's students from the 1960s, conducted in 2000.

Patterson, go against the image of Tinbergen as the ingenious experimenter – untidy is rarely meant as a compliment, however they do point to an intimate connection between his observation style and his analysis. Following quickly on this is a mention of how in 'these days' (the 1960s) the scientific climate has evidently changed towards a more quantitative outlook, rather than the qualitative approaches which had characterised Tinbergen and his school's work in the 1950s.[35]

Patterson's observation that Tinbergen so quickly 'saw from the animal's behaviour what was going on', is clearly intended as a reflection on the great man's observational skill. However it can also represent a comment on the extent to which he had become comfortable with his own system for classifying behaviours, which may have led to its relatively uncritical application in the instances Patterson is criticising. Patterson's thoughts also point us back to the kind of subjectivism discussed in the previous chapter and how integral it was to his field practices. Observation with the subjective element included was a part of the practices, even when subjectivism was written out of the accounts of his methods. When we look at his fieldnotes we can see how observations and analyses met, and how his observations were the stimulus for his analytical work. In the fieldnotes below we can see him switch from observation to hypothesis, to methodological question and back to observation, without substantial breaks, though the annotations seem to have continued over at least two days:

> 27 April 1952 Scoulton Mere
>
> In the afternoon I observed one complete copulation from c.[36] 8 yds. Introduction by begging both ♂ and ♀, the male with "down–up"

35 In the same quote, Patterson reminds us of another aspect of Tinbergen's working style, which is his uncomfortable relationship with quantitative work. Tinbergen's work did always include an element that was quantitative, and this is supported by fieldnotes, in which he clearly considers both qualitative and quantitative approaches: 'That brings us to another point of method: judging intensities. This ♂ was certainly under motivation but what type? Merely quantitative diff with other rit's or also qualitative?' (Tinbergen, 27th April 1952). However, there was a consistent anti-quantitative streak that ran through his research, as Ian Patterson outlined to Kruuk:

> 'I can clearly remember him saying that "this is really quite silly and unnecessary but that is the way it is going these days, you've got to have quantitative data these days before you can get it published", and what he was doing was purely for that purpose rather than a fundamental part of the science.' (Kruuk, 2003:216)

36 In this instance, c. is shorthand for circa.

movements of the head (calling when going down); during the whole copulation ♂ made a rhythmic call, with bill slightly open. Exactly like Herring gull but with ridibundus[37] voice, "with an "r" in it!" I can't help thinking that this is the normal copulation.

This morning: heard the crowing call several times. It must be homologous to the "au call"[38] of the Herring gull, and may be parental (?).

Method: 1 describing clearly recognizable postures and name them provisionally with names <u>not</u> giving interpret.[39] about causes or functions except when function is seen, as in feeding, building, copulation.
2. Registering movements seen in unambiguous situation i.e. fights, copulations, incubation, ♂ feeding ♀ etc.
3. Same in situations where a mixture of drives might be involved: meeting of postures.
4. Compare all situations in which a given movement occurs and see what is common to them all: i.e. head flagging[40] between postures and during fight. Leads to hypothesis that in fight <u>it</u> is an appeasement gesture, submissive. I saw 29 April: A fight with B, in course of fight flies up and lands 2 yds away, not beaten. This brings him too near a terr.[41] holding ♂C, which long–calls[42] while A is still in the air. Still in the airs, A <u>head–flags to C</u>, [43]then forwards to B and attacks B straightaway.

37 Larus ridibundus is the Latin name for the blackheaded gull. The sheaf of notes that these were drawn from were Marked 'Some Blackheaded Gull notes,' and included a great many pages all put together with the central theme of being observations on blackheaded gulls, and with fieldnotes from 1952 – 1958 all mixed together, with no chronological order.
38 This seems to be one of Tinbergen's onomatopoeic sound descriptions, though I have found no further references to it in the literature, so this is only at the level of an inference. It clearly was not as widely publicised as many of the other postures and calls which were put into his published work and became widely used in ornithological and animal behaviour circles.
39 This is the abbreviation for interpretation.
40 Head flagging is a set of movements observed in birds in which clearly marked features on their heads play a large role. In blackheaded gulls, for example, it is their Black heads which are drawn attention to by the movement.
41 This is the abbreviation for territory.
42 The long–call is one Tinbergen's standard posture–behaviours.
43 All underlining is in the original fieldnotes, and not changed by me.

> Hypothesis: if hfl[44] is seen in fights, is this done by the bird who is about to be beaten?
>
> Yesterday I saw and filmed a pair of which ♂ when alighting near ♀
>
> was conspicuous by having his wings extremely raised  He further was conspic.[45] in that he did, after alighting, abnormally intense and ceremonial preening under the wing, again and again, each time followed by vicious peck into ground. I think he did little head–flagging and little forward (?) but we must study film for that. His neck was thick when flying away and repeating, he left the pecking out.
>
> That brings us to another point of method: judging intensities. This ♂ was certainly under motivation but what type? Merely quantitative diff with other rit's[46] or also qualitative?
>
> Tinbergen, (27th April 1952, MS.Eng.d.2387.B.18)

This rich and confusing stream of fieldnote writing assuredly needs explication, and I will attempt a brief interpretation here. The very top of the passage gives the date and location for the observations, in this case Scoulton Mere in Norfolk. He follows that with a series of direct observations of a blackheaded gull copulation ritual, describing, for example, the "down–up " movements of the head, and comparing them to the herring gull which he knew so well from his earlier observations in the Netherlands, and which he was then writing up in The Herring Gull's World (1953). He then notes a few more comparative observations between the blackheaded gull and the herring gull– their copulation cries and crowing sounds. On the next page there is a dramatic shift, into what is an outline for systematic observations intended to visually dissect the movements seen or postures adopted in order to understand

44 This is the abbreviation for head flagging.
45 This is the abbreviation for conspicuous.
46 This is a very ambiguous scribble in the fieldnotes, my best assessment is that it is rit's, an abbreviation for rituals. It could be sit's, but I can see no sense in that interpretation from the context.

their context, and compare them to similar movements in related species. He outlines how observations should be made – 'describe giving clearly recognisable names' – but without those names having interpretations implicit. This page follows through the method (which I will discuss below), and continues over onto the next page. Abutting the very end of this outlining of a methodology are his observations from the 29th of April, two days later in which he describes a fight possibly over territory between two birds, A and B, which induces a conflict with bird C. Tinbergen records some of the postures and gestures assumed by the birds in this squabble, in which he then hurls out a hypothesis, stated in such clear terms: "*Hypothesis: if hfl*[47] *is seen in fights, is this done by the bird who is about to be beaten?"* (my italics). Without immediately seeking to answer that question Tinbergen then records what he saw and filmed the day before, about the gestures and postures of alighting birds, before switching back to a methodological question – how to judge intensity in displays, and with that whether there were qualitative or merely quantitative differences between rituals and between birds.

Undoubtedly this dense passage throws out an enormous number of questions for analysis, but principally there are a few key notes to be made, firstly whether this is a public or purely private document, which is difficult to answer though there are several indications from elsewhere in the fieldnotes that they were treated as public documents within the school.[48] Secondly we must note between the lack of distance between observation and hypotheses as it is quite clear that hypotheses could be as much throwaway questions as thought–out scientific projects. One observation on a fight, for example, makes him speculate whether the gesture of Head–flagging might be some form of submission gesture. The methodological questions at the bottom are related to the observations he has just made: how to judge intensities in a display, when he can see that one bird is clearly operating at a high intensity.

The main methodological instructions that Tinbergen is writing in his notes here are

47 This is the abbreviation for head flagging.

48 There is evidence that Tinbergen was in the practice of fieldnote sharing– either looking at others' notes, or sharing his own. In his notes from the week after his note on method, he remarks: 'The pair on the bank was tested with a mount, see Rita's notes ("incredibly funny").' (Tinbergen, May 5th, 1952) which is certainly suggestive that fieldnotes were substantially seen as semi–public documents.

profoundly interesting as they set out quite clearly how he identified behaviours, a system based largely on observation and comparison. Initially there is the observation, the naming of a particular posture after its identification by the observer. The only standard that he sets is that a posture must be '*clearly recognisable*'. This is very far from an entirely objective standard; it is rather an intuitive test, indeed a social test even where the observation is individual. *It is a social test even where the observer is watching on their own because to be clearly recognisable is to be recognisable in a way that others could identify, even where they are not present.* The next instruction is to name that posture in a neutral way with respect to its function, which is to say that the posture must be identified before a function or a cause should be suggested. By abstaining from including a function in the initial description a posture can be seen as an observable phenomenon, comparable to an organ for a morphologist searching for homologies.

Section 2.2 The Importance of the Comparative Method and the Comparative Morphology heritage

Homology itself is a notoriously slippery concept, covering a variety of significantly different ideas, which function at different levels of biological organisation (see Griffiths, 2006). Homologies are 'relations of "sameness"' (Griffiths, 2006:5; Brigandt, 2002), which suggest that two biological structures are, on a fundamental level, the same. They were seen in Darwinian interpretations of anatomy as being demonstrative of the evolution of different species from single ancestors. The underlying interpretive flexibility in the concept, as demonstrated for example by Griffiths,[49] could have been what allowed Konrad Lorenz to use that as a model for

49 The difficulty and complexity of the concept of homology is neatly illustrated in this philosophical consideration of their definition by Paul E. Griffiths, in which he emphasises the relational nature of the knowledge contained. There is no measurement of similarity or difference, only hierarchies of similarity and difference:

> Homology Defines a Hierarchy of Sets of Characters. Like biological tax, the homologous parts of organisms form groups within groups. The wing of a European house sparrow is homologous to the wing of a Flamingo – both are avian wings. The avian wing is homologous to the forelimb of a lizard – both are tetrapod forelimbs. The tetrapod forelimb is homologous to the pectoral fin of a sarcopterygian fish both are instances of the anterior paired appendages of Sarcopterygii. None of these relationships is a matter of degree – the avian wing is not more or less a homologue of the pectoral

his behavioural work. Lorenz, like Tinbergen had been trained in pre–World War II Europe, in which the concept of homology was regarded as an essential part of the intellectual equipment of any zoology student. Lorenz and Tinbergen built on this training by recognising that individual behaviours could be seen as merely another level of the properties of an organism or species. This is the basis of their interest specifically in innate behaviours rather than learned behaviour, as in the early period they saw innate behaviour as unarguably a property of the species they were studying. Both Lorenz and Tinbergen explicitly sought to draw together the morphological and the behavioural concept of homology (Lorenz, 1971:16; Tinbergen, 1951:189).[50]

Nisbett, in his biography of Lorenz encapsulates nicely the way that Lorenz tried enthusiastically to apply the methods and ideas of comparative morphology to animal behaviour in the 1930s and which influenced Tinbergen and his school:

> The Department [anatomy at Vienna University] chosen by Konrad, the student, was as close as he could get to the study of Darwinian evolution and still be in the Medical Faculty. He studied comparative anatomy with a will, and Hochstetter, at the time Director of the Institute also taught him to reconstruct genealogical trees from the similarity and dissimilarity of anatomical characters – and continued to advise him when he later sought to apply the same methods of comparison to the study of animal behaviour. (Nisbett, 1976:28)

Nisbett's biography, built on interviews with Lorenz, and prone to the flaws of any serious study that relies on the recollections of the individual under the biographers gaze, is in this instance illuminating. Much of the most interesting work, even of the later Tinbergians, would have many shared characteristics of this type of morphology

> fin any more than the class Aves is more or less part of the Sarcopterygii or a sparrow more or less a bird. The scientific practice of identifying biological taxa and that of identifying homologies both originated from the realization that apparently very different organisms or parts of organisms may in fact be modified instances of the same thing, with the result that general knowledge about the more inclusive kind can be sought using the less inclusive kinds as instances. (Griffiths, 2006:5)

50 The late date on this reference is because I am working from the 1971 translation, the original was published in 1941, and was of course not translated from the German during wartime.

as it sought to describe behaviour as though it were an organ of the animal. It was this that made it possible for ethologists to feel that they were making a contribution to a distinctively evolutionary science (c.f. Burkhardt, 1983c) as they could then make phylogenetic statements about the relatedness of species based not only on their physical morphology, but also by treating the behaviour of species as a further "organ". This relied entirely upon their premise that they were studying innate behaviour, and that this innate behaviour could be transmitted across generations of a species, and therefore used as a marker of relatedness. In a letter to Mayr, Tinbergen describes the complexity of making use of the term homology in his research, and clearly recognises the difficulty the term poses, but at the same time its indispensability for his project in that period:

> We seem to find that many movements may be combinations of parts of two entirely different patterns (usually intention movements, e.g. of attack and escape or defence). Since the intention movements are often the very first links of a chain, and consist of mere locomotion, a combination of elements of "going towards" and elements of "going away from" may occur as a consequence of different types of motivation. An animal can go towards another to attack it, or to mate, for instance. A movement which is the consequence of attack + escape might therefore be formally the same as one which is the consequence of mating + escape, and yet the origin of these two compound movements may be different, and we should not, I think, call them homologous. I know that the concept homologous is tricky, yet I think we must use it in this stage, as indicating that two movements stem from the same movement in the ancestor (I understand this concept underlies Spieth's work). The use of "homologous" in this historical sense has, I think, been extremely useful in the comparable stage of comparative anatomy. (Tinbergen to Mayr, May 14, 1953)[51]

This dovetails very nicely with what we saw above in the passage from Tinbergen's

51 HUG(FP) 14.17 Box "Correspondence with Konrad Lorenz and Niko Tinbergen." Folder 1953–4

fieldnotes, which had come from the previous observation season,[52] and in which he clearly was making use of the concept of homology. He even makes explicit use of the idea of homology for the study of behaviour in The Study of Instinct (1951:189). As he goes on to explain to Mayr though, doubts are growing over its usefulness and applicability to animal behaviour:

> My ideas about everything connected with homologisation of behaviour elements are at the moment kind of fermenting... I thoroughly disagree with Mrs Haldane,[53] who says homology has lost all meaning since it has been shown that "homologous" organs of two species may have quite different genetical bases. I think that this is changing the homology concept in a sterile direction, due to an urge to base it on something non–historic, something open to direct observation in modern animals. Alternatively, if the homology concept would move in that direction, and then be discarded as useless, we still need a concept and a term indicating common origin. (Tinbergen to Mayr, May 14, 1953)[54]

In spite of his reluctance to let go of the concept of homology, after this period Tinbergen did turn away from this focus on homologies, indeed his school's most famous work would make little direct use of it, though it would remain as a heuristic and pedagogic tool for his later comparative studies. In conversation with his field students he clearly made use of the homology concept, and certainly he saw the identification of behavioural homologies as being a way of showing evolutionary relatedness.[55] Intriguingly, after his retirement when he was reflecting on his own

52 Observations on gulls in Britain have to fit with migration patterns and similar considerations, such as breeding seasons which broadly run from May to September (varying from species to species). This of course fitted conveniently with the term–time obligations for teaching at Oxford that Tinbergen had, which left most of the summer free for research. Thus most of his fieldnotes follow this seasonal pattern beginning in May and ending in September, with the exception of those few done overseas, either in South Africa or on the Serengeti.

53 "Mrs Haldane" here refers to Helen Spurway who was the great geneticist J.B.S. Haldane's wife. Both Haldanes were noted sceptics and antagonists towards ethology, indeed Peter Klopfer reflecting on the period in his autobiography describes both Haldanes as 'antiethologists' whose communist convictions meant they viewed ethology (because of Konrad Lorenz) as 'a thoroughly Nazi science' (Klopfer, 1999:9).

54 HUG(FP) 14.17 Box "Correspondence with Konrad Lorenz and Niko Tinbergen." Folder 1953–4

55 For example on 5th May 1952 his fieldnotes record that Martin Moynihan had returned from observing Little gulls, and that their behavioural patterns fitted between the blackheaded gull and the tern family, suggesting that was where they fitted in the evolutionary tree.

training, he was rather less complimentary than was Lorenz above, about the role that homology played in his scientific work, indeed he describes it in terms that suggest it was already outdated by the time that he was being taught it:

> That I had not widened my studies earlier was partly due to my own intellectual limitations, partly to the fact that I started my studies at Leiden at the tail end of a period of the most narrow–minded, purely "homology–hunting" phase of comparative anatomy, taught by old professors just before they were succeeded by the younger generation. (Tinbergen, 1985:438)[56]

Tinbergen was an integral part of that younger generation, whose work first looked at stimulation–and–response, and then shifted to describe adaptive features of behaviour, but his work, especially at its most comparative, was clearly influenced by this morphology thinking. Tinbergen's most morphological work treated individual behaviours as morphological features which could be compared across species without any perceived difficulties, and which could be indicative of common descent.

May 5th

Today watched same pair for the 3rd day. ♀ had progressed, she shows everything she did before but in addition food–begs. ♂ is distinctly less reprod. Today, he displays less vigorously and attacks ♀ viciously now and then. Got beautiful films and stills from there, also from collecting birds. Martin back from Holland, saw the essential things of little Gulls, perfect. Little Gulls exactly in between Bl h gulls and terns. General picture therefore begins to take shape: when pair meets, the coming together is the only sexual thing: long call, forward, preening and groundpecking is all hostile, (ground pecking is equivalent of grass–pulling); hfl is submissive, perhaps not sexual at all. (Tinbergen, 5th May, 1952)

This is a very illuminating passage, interweaving the direct observations with the fleeting records of camp life. Martin Moynihan has returned from observing little gulls (*Larus minutes*) and evidently Tinbergen and he have been discussing the contrasts in behaviour patterns between the little gull, the blackheaded gull and terns. Their resultant decision is that the little gull has elements similar to the blackheaded gull and the tern (*Sternidae* family), clearly an important set of discussions when we recall the aim of using behaviour as an ally of taxonomy and comparative morphology. In this case the little gull, it is suggested here, fits a classification somewhere between blackheaded gulls, and terns. Tinbergen then switches straight back to the story that he was recording above his interjection on Moynihan's observations, watching a blackheaded gull pair over a few days and recording their mating behaviours, and their curious mixture of apparently sexual behaviours, combined with aggressive behaviours.

56 Kruuk also uses Tinbergen's description of his time as a 'homology–hunting' student and states that for Tinbergen university biology in that period 'consisted of lists of facts and dry comparisons, contemplated in endless lectures in stuffy rooms', (Kruuk, 2003:39).

Tinbergen's exact view on homology in behaviour is somewhat opaque, perhaps reflecting the internal complexity of the concept itself, which Griffiths demonstrated above. Indeed he recognised problems with applying the concept to behaviour himself, even very early on in his work (Tinbergen, 1951: 190). There were two route out of the problems of applying the idea of homologies that Tinbergen suggested firstly through trial and error – essentially whether a homology is 'identified' seems to have been a question of whether it seems to be similar enough to him as an observer (Ibid.). Secondly he emphasised the importance of identifying fixed patterns of behaviour, such that these fixed patterns can be compared across different species, and from there homologies inferred. In this respect he directly compares fixed behaviour patterns to organs in comparative anatomy: 'they play the same part as 'organs' in comparative anatomy' (Tinbergen, 1951:191). However he never goes into more specifics about exactly how the analogy between comparative anatomy and behaviour was meant to work, instead falling back on a the idea that homologies would emerge from: 'purely descriptive study' (Ibid.). This lack of definitional clarity, depending only on the eye of the observer for a definitive identification, meant considerable flexibility in possible application. However it also meant that Tinbergen's work was open to criticism for arguing that homologies could be drawn between behaviours in two different species even where no common origin for them was known, a point made by Lehrman (1953) in his critique of particularly Lorenz's ethology.

Section 2.3 The development of ethograms as fundamental objects of comparative study

In the field Tinbergen's work focused on identification of separate behaviours, because he saw them as something akin to 'organs' of behaviour (Tinbergen, 1951:191). This qualitative aspect of the Tinbergians's work, which closely followed the model of comparative anatomy, Tinbergen felt had primacy over quantitative work. Underpinning this qualitative approach was the aim of total description and classification of all of a species' behaviours. The completed list of a species' behaviours he called the 'ethogram', and in the early years of the school constructing

ethograms was the driving ideal of the whole school. The ethogram was to be the basis for full behavioural–morphological comparison which would then help fit behaviour into the comparative anatomy mode of practice, which both Tinbergen and Lorenz saw as its model. The ethogram was only built after extended observation periods so as to ensure that they had seen all aspects of behaviour. First there was a lengthy period of observation in which all the actions or movements that an individual animal could make or perform were recorded. After this they were recorded in a coded form in order that patterns could emerge. These patterns, which have subsequently been called Fixed Action Patterns[57] (see for example Thorpe, 1979: 100) usually abbreviated to FAPs were therefore seen as indicating specific *behaviours*. It was only repeatedly observed combinations of labelled actions, gestures, or muscle movements which are the FAPs, and it was the complete list for an individual species of these FAPs which was the species's ethogram. The distinction between a movement or action on the one hand and a defined behaviour on the other is a crucial conceptual one as it was only these defined behaviours which could be fitted into ethograms. Unfortunately all of these terms were used interchangeably by the Tinbergians themselves so the distinction in terminology is one that I have introduced for the sake of conceptual clarity. The fieldworkers' manner of generating ethograms was built on long periods of direct observation in the field. During these field studies behavioural traits were observed and named and then studied in relation to the order that they occurred in fixed behaviour sequences. Tinbergen insisted that the level of detail of these observations should be extraordinarily high, suggesting that his observers should record movements at the muscle–by–muscle level: 'the ultimate aim of our description must be an accurate picture of the patterns of muscle action' (Tinbergen, 1951:7). Looking for these patterns was as much the business of the field as the laboratory, and when Tinbergen

57Interestingly although it is many times attributed to Tinbergen's The Study of Instinct, (1951); he never actually uses the phrase Fixed Action Pattern, he uses the terms 'fixed pattern' (1951: 87) and Innate Motor Pattern, (1951:137). I have yet to attribute it correctly – it may come from another work of Tinbergen's, or from a fellow biologist, but he has clearly become identified with it more strongly than any other figure. It seems to have passed into the folk memory of biologists however that the phrase Fixed Action Pattern comes from that part of Tinbergen's writing – for example see Reilly (1994:707); Buss et al. (1998:533), both of whom cite the Study as being the origin of this phrase. Indeed a google search of the phrase “Fixed Action Pattern” Tinbergen indicates many hundreds of citations for 'Tinbergen 1951' and links to the Study of Instinct, suggesting just how far this mythic link has penetrated.

set out how to observe and construct an ethogram in the Study of Instinct he drew no explicit differentiation between how one should be constructed in laboratory or field:

> *Ethograms*
>
> Special emphasis should be placed on the importance of a complete inventory of the behavioural patterns of a species. It is a natural tendency of the experimental worker to select a special problem, as, for instance colour vision, or homing, or the delayed response. This specialization is often accompanied by a narrow point of view and a neglect of other aspects of behaviour. The resulting generalizations, based on too limited a foundation, may give rise to sterile controversies.
>
> Because of the importance of extensive descriptive work as a necessary preparation for experimental work is not generally realized, I shall give some instances of these controversies… (Tinbergen, 1951:7–8, Italics in original)

Tinbergen emphasises here the importance of constructing the ethogram through very detailed and observation and description. His writing has more than one target, however, as he is seeking not only to outline a 'how to', but also to argue that broad study of a species behaviour is a necessary precondition for any causal or quantitative studies. These comments are clearly aimed at the Behaviorists, who were uninterested in collecting the full set of instinctive behaviours as they studied the malleability of behaviour.[58] The main body of the text is his recipe for muscle movement by muscle movement observation of behaviour, which is perhaps closest attained by the description given by Desmond Morris of his laboratory work which we will see in the third chapter, but is at least sufficiently similar to the fieldnotes, and the accounts of his practices in the secondary literature above, that there is definitely a sense that this was the Tinbergian ideal, even if in practice his approach tended to be much more intuitive, and followed his unique talent as a field observer.[59]

58 In fact to emphasise just how multi–vocal the text is, there is also a note of disapproval toward Karl von Frisch's work, as Tinbergen's mention of 'colour–vision' is perhaps pointing towards Frisch's work on bee vision, and maybe Tinbergen's own youth studying homing instincts and colour vision. Both of these studies looked only at a very small part of the life of the animal under study rather than looking at the whole and trying to build an ethogram prior to experimentation.

59 Patterson's quote in the previous chapter is one example – another is Bolhuis, a present day

Tinbergen's background, as we saw in the previous section was an observer amateur observer and naturalist before they arrived at the school, but nevertheless he did not try to found a discipline purely on their 'observer–skill'. Instead Tinbergen sent his students out with the intention of their building ethograms, with the associated heritage of comparative morphology, and following more or less closely Tinbergen's own writing on methods.

Section 3: "As the Gulls might say"

The title for this section very much sets the tone for what I will be investigating, and it comes from Tinbergen's Scolt Head Island fieldnotes. Although this is from his scientific fieldnotes it is self–evidently demonstrating an anthropomorphic perspective. This perspective is, I will argue in this section, frequently one of the modes in which he wrote his fieldnotes, but it is particularly interesting because as we saw in the introduction to this chapter, his official antipathy toward anthropomorphism was well known. His initial British field observations were on herring gulls, culminating in The Herring Gull's World (1953), but the arrival of increasing numbers of students gave him the opportunity to broaden his studies across other species of gull, as he explained to Ernst Mayr in a letter in early 1952:

> You know that I have been doing some work on social organisation of Herring Gulls during a number of years. I have at last written up the results in a coherent account, which will appear as a "New Naturalist" book next spring. Most of my work has been concerned with unravelling the relations between individuals and between pairs, and I have also spent much time in some experimental work on releasing stimuli, of which the food–begging–response work was the most complete part.
>
> I now begin gradually to become deeply interested in comparison of the Herring Gull with related species, in the way Lorenz has been working on his duck. I believe we can, by combining the causal analysis

ornithologist describing Tinbergen as a 'Brilliant birdwatcher' (Bolhuis, 2004:1140).

> of signal movements with this comparative work, find out much of interest. (Tinbergen to Mayr, July 20, 1952 Mayr archive)[60]

Tinbergen's book was indeed published as a *New Naturalist* book, a popular post–war series aimed at giving a general introduction to the natural history of a species, set of species, or ecological niche, such as Hedges (Pollard et al, 1974), Wild Orchids of Britain (Summerhayes, 1968) or Snowdonia (North et al, 1949).[61] Following the plan that he had suggested above Tinbergen did start to research different gull species related to the herring gull, beginning with Scolt Head Island's blackheaded gulls. His Scolt Head Island fieldnotes provide an interesting window on the early period of the school, even though his brief sojourn to the island was somewhat disastrous with exceptional high spring tides repeatedly washing the nests of the breeding birds away (c.f. Kruuk, 2003:168). In his fieldnotes Tinbergen describes the sensation of watching this:

> 6. pm I see the tide coming in the creek near my hide it seems still at least 2 ft below the surface of the saltings. But it is running in fast (silently and treacherously as the gulls might say). In strong contrast the gull dozing at its nest! (Tinbergen: Monday, May 21 1951, MS.Eng.e.2749)

In the middle of this observation there is a switch of point of view, from that of the scientific and 'objective observer' who notes the time, the distance that the tide has risen to one whose tone has radically shifted, talking about the treacherous nature of the tides from the point of view of the birds, asking in effect what *the gulls might*

60 HUG(FP) 14.7 Box 11 folder 479.

61 In his history of the series The New Naturalists (2005) Marren identifies Tinbergen's contribution as at the same time one of the most successful and one of the most unusual of the series:

> The trouble, from the publisher's point of view was that The Herring Gull's World did not fit well with the other books and seemed a better candidate for the university press. It did not pretend to be a complete biology of the herring gull, and in those days behaviour was regarded as a specialised and arcane field. (Marren, 2005:203).

Marren went on to explain that Tinbergen's book was given rave reviews and went on to be the second best selling book in the series which to date includes 95 monographs, and which is still commissioning new books (Marren, 2005:203). Tinbergen's herring gull work therefore managed to capture the interest of the general public in what was seen as the arcane field of animal behaviour. However the herring gull work, as he had explained to Mayr above, was to be the springboard for his comparative field research.

say. This is the point at which Tinbergen slips into either subjectivism or anthropomorphism, or both. It is subjectivism, because, in almost a Cartesian way, *a thought presupposes a thinker,* and here the thought is of the treachery of the seas. Arguably it is also anthropomorphism because the thought is intelligible because it is expressed in simple human terms, rather than trying to explain the cognitive and/or emotive processes of the bird and therefore how they would subjectively see the world. Attempting to explain how animals see the world was a live scientific programme in this era, the legacy of the great Baltic German animal physiologist Jakob von Uexküll who had wanted to understand the subjective perceptual world of the animals he was studying; this subjective perceptual world he called the *Umwelt* (e.g. von Uexküll, 1934). Tinbergen however had *officially* bracketed off questions of animal subjective experience as of no utility for understanding the causes of behaviour: 'Because subjective phenomena cannot be observed objectively in animals, it is idle either to claim or deny their existence' (1951:4). Indeed he went on to argue that this kind of subjectivism is little more than guesswork:

> Hunger, like anger, fear, and so forth is a phenomenon that can be known only by introspection. When applied to another subject, especially one belonging to another species, it is merely a guess about the possible nature of the animal's subjective state. (Tinbergen, 1951:5)

Tinbergen along with other scientific ethologists,[62] in their academic writing, strongly opposed trying to understand animals' subjective worlds, and sought to preserve and present an image of objectivist observation (see Crist 1999:172–185). However as the title of this section reminds us, this presentation far from encompassed the whole of their practice. This is not necessarily to suggest that this sort of 'as the gulls might say' subjectivism was a conscious part of the school's research approach. However, Tinbergen's insistence on detailed close observation helped create a situation where subjectivism could play a part in the process of understanding the behaviour of the animals under study. For example to understand what stimulates a certain behaviour, one must see what is relevant and what irrelevant in the environment of the animal,

62 For example Lorenz also publicly condemned anthropomorphism and the imputation of motivations to animals (Lorenz, 1950:231).

and therefore what could be the stimulatory cause. This is precisely the process outlined by the subjectivist von Uexküll (1934) for beginning the study of animal subjective states. It would be possible to list all the potential stimuli of a certain behaviour and the Tinbergians did do this, making long lists of movements and searching for patterns in those lists (see Morris, 2007:74). Anthropomorphism and subjectivism, however, did represent convenient short cuts to understanding, as they replace lengthy studies with a moment's imagination or intuition of what it might be like to be the animal under study as was implied in Ian Patterson's criticism of Tinbergen in the previous section. The accuracy of that intuition was of course open to question, and every movement could have had a very large number of different possible interpretations, a version of Quine's theory of underdetermination (Quine, 1964) amongst the ornithologists. To try and avoid relying upon these intuitions, Tinbergen set out a range of instructions in his fieldnotes. He never directly states that these were for anything other than private consumption, but it is also possible that these notes were written for his students who were observing in the field at the time. [63] Whether these sheets were intended to be purely private or for circulation amongst his students, Tinbergen's advice is clear:

> Do not merely try and get certain restricted statistics, but keep trying to understand the general problem "what makes the bird adopt this posture?" Also keep looking at <u>every</u> thing a bird does, whether postures, feeding, fleeing etc. –
>
> Never forget that an unexpected thing (something against predictions) is always worth closer study – it need not all invalidate principles on which prediction was based (although it may) but it may mean (and usually does mean) that you had misjudged the causal situation, (e.g. a new strange bird has entered the situation, or something similar). (Tinbergen,

63 Tinbergen's tone could suggests that these notes were meant to be read and used by his students in the field They are all written in the imperative 'try to get statistics…' (Tinbergen, 'Blackheaded gull notes', 1951:1 MS.Eng.d.2387.B.18), or 'Clarify oblique in "normal"…' however as there is no other marking on these sheets, and no one else's handwriting it is impossible to tell absolutely whether they were used by anyone other than Tinbergen himself. The passage in the main text above is the most suggestive– 'Never forget that an unexpected thing', perhaps indicates that it was intended for students, as it is phrased more as advice than reminders to self, but even here it could be interpreted differently.

'Blackheaded gull notes', 1951:4 MS.Eng.d.2387.B.18)

The instruction here is that the striving should be toward understanding what stimulates a bird to behave in a particular way; this classic stimulus–response finding is what Crist describes as part of the mechanomorphic language of classical ethology (1999:9). Tinbergen couches this question in a way that puts the individual behaving gull at the centre of his research project, instructing those who study it to consider what possible causal factors, such as the arrival of other birds, may have provoked these responses. These instructions support Crist's idea that Tinbergen's work is a nearly pure form of mechanomorphism, for example: 'for with Tinbergen's gulls no feeling links the birds, no atmosphere envelopes them. The gulls are not presenting their displays; rather, they appear as pawns in the irresistible grip of occurrences they can neither control nor comprehend' (1999:184). Tinbergen's instructions, which point to his interest in every seemingly minute aspect of their lives – their feeding, postures, fleeing – all mean that he wishes to consider all the possible causal stimulations of these mechanomorphic automata. However, and perhaps surprisingly, they also provide the intellectual setting in which subjectivist field observations were made.

Tinbergen's fieldnotes switch easily from the kind one would expect were one to follow the instructions given above, to those which have a very different feel, either because of the quality of their social description (as we will examine in the next section), or from attribution of feelings to the birds studied. Undoubtedly there are pages of numbers and coded behaviours, which are designed to lead to generic and generalisable descriptions of behaviour that Crist's work would lead one to anticipate; however there are also comments on these pages which show how complex the interaction between the Tinbergians and their birds could be, for example:

June 1, 1951
At 9.20 a.m. relieve Martin in hide. I make it face nest 3, and can see 1 to right. M says they were jittery, which is surprising since yesterday they

> were very tame.
>
> 10.40 [dutch] It is amazing how this bird keeps whole neighbourhoods nervous. Possibly it is one of the birds which stood yesterday and stares where my hide is near. It alternated kek[64] with a hoarse but soft werrer. I don't know what sound that is. It may be that it is mate 3 but I don't think so since 3 on nest is perfectly calm. (Tinbergen, 1951, MS.Eng.e.2749)

The key word for me here is *jittery*. Tinbergen's observations are normally only of units of behaviour, made up of definable sounds written in an onomatopoeic format, or described postures. However his choice of jittery, and indeed his description of the *nervous neighbourhood* that follows is quite different to the coded behaviour descriptions that Crist's analysis would lead us to expect. Instead they are descriptions of either moods or emotional states of individual birds or groups of birds. These are entirely the type of inferences that he publicly stated should be avoided, as they are not directly observable postures, movements, or sounds, but instead are inferences about the subjective emotional state of the birds he observed.

Tinbergen's fieldnotes provide plenty of further illustrations of this type of subjectivism. For example he described watching a very aggressive male bird:

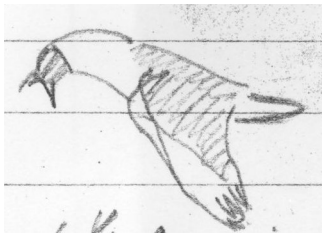
> Thursday 28 March 1957 with Gilbert in valley hide 4–6pm
>
> I follow one highly aggressive ♂, he is alone. Is visited by a ♀ twice (same??). Forward: I see 11 cases of straight forward[65] in him followed by attack on another bird – which had not postured back & stayed. In 27 cases he did proceed → other in straight for but the other retreated. Saw 4 up–forwards,[66] and none of these was followed up by attack. Saw many doubtful cases. When ♀ alighted he was slightly up, she very much so.

64 Both kek and werrer later in the line, are onomatopoeic descriptions of the sounds made by the gulls. It is a very common device of Tinbergen in the fieldnotes, as it records relatively simply the sound made during a particular behavioural context or situation. Another very common sound he records is the krekrekre call (e.g. 3rd March 1958), and the famous kittiwaak of the kittiwake.

65 "Straight forward" is one of the standard defined postures that Tinbergen recorded for his birds. He rarely uses the word posture or more formal descriptions in his fieldnotes using only the shortest possible descriptor.

66 Like the "straight forward" the "up forward" is another of Tinbergen's standard defined postures. See Tinbergen, 1958: 61 for some examples from various different Laridae (gull) species.

Both times he attacked her. Once the ♀ gave the first peck (vicious, on his face) – she had forwarded up extremely just before; it looked as if she pecked in self defence, but why? The peck made him furious, and he gripped her firmly in neck & dragged her along for about 10–12 secs!
This same ♂ showed 6 times the attack call, always with at his hfl neighbours. In 5 out of 6 cases it was in the "head down oblique" (in 3 cases wings ahead)


head down oblique

In 6th case in something between this and forward.
Saw one long static flash with ♂ A in normal oblique, ♂ M in anxiety oblique. ♂ A had taken initiative and B had retreated a 6" or so, the anx obl.[67] was correlated with thin neck, neck away from A when or sideways,


and jumpy when A moved suddenly. Finally B walked away.
(Tinbergen 28th March 1957, MS.Eng.d.2387)

This extract from Tinbergen's fieldnotes is a fairly typical one, it has the date, a few hand sketches of postures, and a series of descriptions of those postures, along with the number of times that posture was observed. In amongst all of this relatively objective data, there is also noticeable use of subjectivist language. The crucial passage is at the top during the first fight between male and female birds. The key word is *furious* as this is where he slips from what is by the standards of the day overtly objective, to what is (depending upon your interpretation) either a description of the internal state of the bird (subjectivism), or a suggestion of what the bird might

67 "Anx. obl. Is Tinbergen's shorthand for the anxious oblique posture – a variation of the oblique posture. Oblique and anxious postures are discussed in Brown, Blurton–Jones and Hussell, (1967). It should also be noted however, that the title of this entire posture has a high level of subjectivism built in as anxiousness is not a positional quality but an internal mental state.

have been feeling, had it been a fully emotional human being (anthropomorphism).[68]

The two illustrations of Tinbergen's use of subjective language in the field I have shown above (the jittery/nervous neighbourhood extract, and the furious extract) are far from the only "positional slips" in Tinbergen's notes, but that they are there at all should be a surprise to those familiar with his professed opposition to anthropomorphism and subjectivism. With the addition of the quotation giving this section its title – "As the gulls might say" – it is very hard to argue that Tinbergen in the field did not slip into either subjectivism or anthropomorphism on regular occasions. Checking through the fieldnotes it is clear that there is widespread use of subjective and/or anthropomorphic terms, not perhaps on every page, but certainly with regularity through the notes.

Subjectivism and anthropomorphism were Tinbergen's public *bête noire,* all but absent from their scientific writing, as Crist (1999) demonstrated over the course of her book, but they were vividly evident in the fieldnotes. They have been written out of the professional descriptions, but as will be investigated in chapter five they do reappear in some of the more popular literature. Most importantly, though, they are subsumed into the 'enigmatic' quality that Crist describes in Tinbergen's professional scientific writing (in this case she is talking about his work on butterflies):

> At the same time that gestures are extinguished, replaced by mathematically[69] described movements, Tinbergen also characterizes the movement of the antennae as "remarkable" and "bowing" as a "spectacular display" and "a perfect and elegant finale"; he observes that

68 Interestingly Crist notes that Lorenz, Tinbergen's fellow ethologist, and a fellow campaigner against anthropomorphism specifically attacked the use of the words fury and furious as being far too subjectivist to be used by an ethologist (Crist, 1999: 220). I have found nothing in the Tinbergen – Lorenz correspondence about it, so I can only presume that Lorenz was not specifically attacking Tinbergen's field practices, as there is no evidence that he would have known of Tinbergen's use of these words in what were Tinbergen's unpublished notes.

69 The use of the term "mathematically" suggests to me that Crist is following the approach of Mike Lynch (1988) on mathematization, a term I will explore more fully in chapter 3. However she does not make this link directly herself, even though she does reference some of Lynch's other work, so my suggestion cannot be directly confirmed. I can only note that her use of the term 'mathematically described movements' is meant to convey a sense of cold objective precision which she is directly opposing to the joyful and subjectivist accounts of Tinbergen's naturalist forbears .

> the male butterfly closes the "wings extremely slowly – as it were, 'with emphasis.'" What is it that makes the antennae's movements remarkable or bowing spectacular? And how can the closing of wings be emphatic without implying that their closing is meaningful in some way? These exclamatory remarks point to some enigmatic quality of the display that, while present to the viewing, is actively kept outside the writing. (Crist, 1999: 197)

For Crist then, it is the later writing process that is significant. The description is king, because it is here that all sense of life and vitality is removed, and replaced with what she calls mathematically described movements. Indeed, she illustrates her case with a perfect example of Tinbergen's prose, filled with mathematised description of a butterfly's 'longitudinal axis' and its '45 degree' relationship with the ground. As it is such a good example of Tinbergen's published literary writing; I shall follow her in reproducing it here in full:

> During quivering, the antennae of the males are spread horizontally and at right angles to the longitudinal axis of the body. As soon as quivering develops into fanning, the antennae begin to perform a remarkable movement. Held completely stiff, they make a conical sweep so that the tips describe a circle. Both antennae move synchronously and in the same direction, that is, back–upwards–forwards–down. Gradually this circle becomes an ellipse with its longitudinal axis inclined forwards and upwards, making an angle of 45 with the ground. The downward movement is clearly faster than the upward one. Also the antennae are gradually directed forwards. We observed one male in which the antennae rubbed against the legs of the female, but this is by no means the rule. Each complete circling lasts about ¾ sec. a bout of wing fanning and antennae spinning can last from 1 sec to several minutes. Fanning is the first to cease when courtship lapses, e.g. when a cloud covers the sun; its tempo becomes slower and finally antenna spinning is also completely suspended. (Tinbergen 1972:210–11)

Within this type of descriptive framework any sense of the subjective has been lost, instead of which there is the mechanomorphic approach that Crist argues is characteristic of Tinbergians. The consequence she argues is that with the shift to mathematised mechanomorphic description of the animal subject, removing the reader's idea of the butterfly as an expressive creature. 'Thus while the description is impeccably precise, it is not the type of description to evoke an image; while it is mathematically precise, it is not visually intimate.' (Crist, 1999: 195)

However Crist's analysis cannot be applied to the fieldnotes which can be both mathematically precise and also contain strong subjectivist notations. Indeed some of the 'objective' postures that Tinbergians observed, such as the 'anxiety oblique', have subjectivism literally written into them. That means that the subjectivism which could be such a useful short cut into the understanding the herring gull's world – the title of Tinbergen's most successful book after all – was not even entirely written out of the published accounts. His descriptions of nervous neighbourhoods and furious birds normally were written out of the professional scientific accounts, but those like the 'anxious oblique' enshrined in postures remained. More significantly though, the fieldnotes which included these subjectivist terms remained the basis for Tinbergen and his students' work, and so although contentious subjectivist words themselves had frequently been excised by the time of publication, lessons drawn from those same observations remained.

It is difficult to square Tinbergen's public anti–subjectivist stance with his private fieldnotes. When he came to publishing his professional academic literature he tended to avoid the kind of simple subjective analyses that appear in his notes. It remains the case that he was, in public at least, vehement in his belief that the subjective world of birds was both unknowable, and therefore could not be used as the basis for understanding the motivations or cause of an action or behaviour. Should the reader remain sceptical of Tinbergen's use of subjectivism in the field, the next section should provide incontrovertible proof directly from the fieldnotes.

Section 4: The Tale of Casanova

Tinbergen was public in his declamation of the investigation of subjective states of the birds that they were watching, and in ascribing human characteristics to animals. Yet, as we saw in the previous section, there was frequent use of this kind of language in his fieldnotes, every time he wrote about animals as jittery, furious or nervous. The next stage, and one which personally I found startling when I began my research in Tinbergen's own fieldnotes was that I believe he began by seeing the social life of the birds as exactly that, *social drama*. One of Crist's major claims is that Tinbergen severs the communication possibilities between his gulls by the manner of his description. She argues that Tinbergen described animals them in a manner which envisions them as automatons and perfectly mechanistic beings. Tinbergen's notes however demonstrate that there is more to the picture than could be hinted at by his more scientific output, indeed it is the richness of these notes that I found so initially surprising. Though he does frequently record his observations in the objectivist manner that he publicly advocated, interspersed with this approach are records of both the social life of gulls, and the effect that watching their social dramas had upon those doing the watching.

The clearest example of the life of gulls being presented as social drama is what I will set out in this section. It comes straight from the fieldnotes and was as far as I can tell never published. Beyond being simple anthropomorphism, this example is social drama of the highest calibre, with all the characters that one might expect of a theatre performance. The argument that I will make however is that social drama, even if it seemed to be written out of the professional scientific accounts, was always something that Tinbergen *saw* in his observations of nature. In fact much of this ethos leaked out in his more popular science presentations, whether in the popular books or broadcasts, as I will explore in the fifth chapter, but in this chapter it is establishing the importance of the social drama of the birds that I will set out.

Tinbergen was interested in the explicitly social aspects of bird and animal life. He published his second book in English on the topic, (Social Behaviour in Animals,

1953a) and much of the first book (The Study of Instinct, 1951) was on this area as well. In this he acknowledges immediately his debt intellectually to Konrad Lorenz, whose work on domesticated animals and pets had studied them both as individual animals in the world, and as groups of animals interacting with each other. Of course the fact that Tinbergen and Lorenz shared, to some extent, theoretical approaches is far from the same as saying that they shared practical methods – it is now almost canonical to stress differences between them by saying that Tinbergen was 'the hunter' in the wild in search of elusive prey; whereas Lorenz was 'the farmer' happier to examine domestic or semi domestic species at home (e.g. Kruuk, 2003: 10–11, 62; Burkhardt, 2007:88). However, there is in Tinbergen's initial approach to the subject a clear desire to explicitly explore and explain the social drama found in animal behaviour. Indeed Crist's idea that Tinbergen felt there was nothing more than stimulation–and– automatic responses operating between birds cannot survive the lively drama of the anthropomorphic tales described in Tinbergen's notes. Her argument is that Tinbergen's language prevented the possibility of imputing meaning or intention to an action of a bird, but his field observations which we will see below, clearly do that very thing.[70]

In his second English–language book, Social Behaviour in Animals, (1953a) Tinbergen made use of the term 'animal sociology' (1953:129),[71] but more

70 The clearest example of Crist's view that Tinbergen broke any possibility of social communication comes from a comparison she makes between Tinbergen and the ornithological work of Julian Huxley. She chooses Huxley as the paradigm of vivid communicative writing, in which anthropomorphism and subjectivism blend in descriptions of behaviour that retain a sense that the observer is enjoying an aesthetic experience alongside a scientific investigation. Crist describes Tinbergen's writing on courtship thus:

> The connectedness of the displays as addressed or mutually orchestrated gestures is deemphasized, if not severed. The severance is a result of the unit of analysis being the isolated display rather than interacting couple. For example, the "Oblique–cum–Long" and the "Upright" are agonistic, while "Turning Away" is a display of appeasement; this is what they signify regardless of the context of their use. For Tinbergen, the meaning of a display is not achieved in use, in accordance to whom it is addressed or for what purposes it is intended, but has been formed and fixed in the course of evolution. The meaning of the isolated display is stable and context–independent. The melange that happens in courtship displays does not yield, as a whole, an expressive gesture, but reflects an underlying conflict between opposing drives (very often , for example, the simultaneously "released" impulses to escape and attack). The function of displays is that they become effective as "signals." However, there is no communicative link between the birds in this analysis. (Crist, 1999:184).

71 A full discussion of Tinbergen's interest in animal sociology will be given in chapter five, when I discuss his interest in humans, and lessons that can be drawn from animal life for humans. The term itself is intriguing however, as it suggests either a willingness to learn lessons from human

importantly he presented a variety of behaviours as having a social character, even using equivalents of the sociological terms of the day. He describes his interest in beginning to understand 'the behaviour of sex partners, family and group life, and fighting. In this way we will discover, step by step, social structures.' (Tinbergen, 1953a:3). To anyone with familiarity with mid–twentieth century social theory, whether of the Talcott Parsons (e.g. 1954) or A.R. Radcliffe–Brown (1952) traditions, the language Tinbergen has used to set out his scientific aims would be far from out of place in either of their writings.

Tinbergen's fieldwork, in which he performs the role of objective observer of social life, without interacting with his subjects and with deliberate scientific distance preserved (in a manner akin to the great anthropologists of the first half of the twentieth century), has attracted a great deal of comment as I have talked about above. However, as the following passage demonstrates, Tinbergen clearly was capable of seeing and describing animal behaviour with great social nuance, almost with the pen of a dramatist. His fieldnotes provide plenty of extant examples descriptions of behaviour which preserve the sense of social drama, in which animals are directly interacting with each other. That these events had a great emotional effect on the observers is also apparent from the fieldnotes as they describe precisely their feelings of watching these dramas. Without question the most vivid of these descriptions is the tale of Casanova, a kittiwake he observed on the Farne islands, and which was probably named by his student Esther Cullen.[72] Bear in mind throughout that Tinbergen here is describing birds:

> In afternoon we watch a tremendous fight between Casanova and owners of nest B. Casanova had plunged on ledge B where 1 bird was sitting, I am pretty certain ♂.[73] They fought by biting each other in neck, face and

sociology, which was a firmly established discipline at the time, or that the study of animal social life could teach lessons for humans. Either of these interpretations suggests that he feels that there is a set of phenomena in animals which can be rightly titled as social behaviour or social life.

72 Tinbergen attributes the discovery of the way to visually identify individual kittiwakes to Esther Cullen, based upon Cullen's observation that kittiwakes have unique wing tip patterns, which they retain through their moults and which she recorded in order to be able to identify individuals on a crowded kittiwake cliff. (Tinbergen 1958:196)

73 Throughout his fieldnotes and laboratory notes Tinbergen uses the standard ♂ and ♀ to denote male and female individuals, and ♂♂ and ♀♀ to denote respectively multiple males and

> beak, and finally Casanova throws other out. C's ♀stands on higher ledge, he "sings", and she comes. Then ♀ owner arrives, and attacks Casanova. In the confused fighting that follows now the two ♀♀ jab at each other over C's neck, who sits in between, and both attack Casanova; for a long time they both squeeze his neck between their bills and he gapes several times "in despair". Finally C's female is thrown off and C and owner ♀ remains, as if in pair.
>
> Then ♂ owner returns. First time he is not even allowed to land. He falls down, swims off, then round and lands. A wild struggle ensues which ends with Casanova being thrown over board. We all applaud: justice has been carried! The pair now indulge in tremendous displ. building.
>
> Tinbergen (3rd May 1954 MS.Eng.d.2387.B.16)

This passage from Tinbergen's fieldnotes was revelatory to me. This is not the Tinbergen I had been led to believe existed, it was far from Crist's cold observer, nor was it Kruuk's hunter–observer, though in terms of an ethologist finding his field niche, it could certainly still mesh with Burkhardt's grand idea of local ecologies of ethology, but in an admittedly unexpected way. There are two key elements that emerge from this passage which run counter to the more standard narratives of Tinbergian historiography which I will explore below: firstly the extraordinary social drama, almost anthropologically thick description; and secondly the attribution to individual birds of their own anthropomorphic character.

Section 4.1 Social Drama

Once the conventions of Tinbergen's fieldnotes are understood, the stark, spluttered prose that is flying from the pen of the observer as he recalls and records what he has seen that day, and the frequent use of a form of shorthand, where frequently used combinations (e.g. displ. building meaning display building) are shortened and visual keys are used (e.g. the ♂ sign as opposed to writing male every time), the drama is apparent to the reader of the passage above. The language is of hyperbole and melodrama – 'a tremendous fight'; 'gapes "in despair"'; 'wild struggle' – and the

females.

sense of narrative is carried throughout. It is difficult to describe social behaviour in animals without recourse to the language of social life in humans, and in the passage above Tinbergen does not even try. These notes were never written up or directly published, and they cannot fit into the projects of objective studies that he did publish because they are unmistakeably anthropomorphic.

The social drama of the piece also draws out why Tinbergen in this early stage in his career was so interested in what he called animal sociology. There is in the social drama of the piece, a level of richness which demands sociological analysis. Once again I fear I must point past Crist in her analysis of the Tinbergian approach, as although it describes much of his hard science publication, it does not encompass the whole of his field practice. Crist argues that:

> Tinbergen does not see the gulls as addressing each other. He instead apprehends each separate gull as going through an involuntary series of motions that are the fortuitous outcome of an inner conflict of psychologically defined tendencies. (Crist, 1999:184)

In suggesting that Tinbergen does not *see* the birds as addressing each other – fundamentally she is arguing that he does not recognise the possibility of social behaviour or communication between gulls – she is mistaken. This of course could only be discovered through the kind of close reading of his fieldnotes, but it is evident from them that Tinbergen, even in the field, retained the sense of the living animal, as an actor in a social drama, as much as a research subject. Indeed this also runs counter to Crist's analysis, in that she argues explicitly that with Tinbergen's description of gulls' behaviour 'no feeling links the birds no atmosphere envelops them.' (Crist, 1999:184). There is something about his portrayal of Casanova, and the vignette surrounding him, that argues that Tinbergen retained alongside the more objectivist observations, a real and genuine affection for his birds, and the capacity to be emotionally affected by their behaviour. This then leads to a play in the tension between Tinbergen's roles as professional observer of animal behaviour, and his background as bird lover. More importantly however, Tinbergen, when writing in his

professional notes, still recorded the social drama of the event, and showed that he saw his birds as directly interacting with each other in that drama.

Section 4.2 Ascribing Character to birds

Casanova is a name which carries with it an enormous amount of social baggage, and clearly this was part of the reason that it was chosen for the naming of this bird. The others remain relatively anonymous, merely the occupants of "nest B" or "C's ♀" (in this case meaning Casanova's ♀) whereas Casanova is the individual at the heart of the drama. Once it was possible to identify individual birds, a breakthrough made possible by Esther Cullen's discovery (which I discuss below) that wingtips were as individual as fingerprints, then observations on individual birds could begin. Crist states that 'the invocation of human experience and the use of lyrical language are all but completely absent in Tinbergen's work on gulls' (1999:180). The evidence from the fieldnotes is that this is simply not the case, Tinbergen could write lyrically about individuals, casting them as actors in social dramas, and in so doing reference names often given to them by his students to reflect their particular characters. He publicly stated that some of his gulls were identified individually, and that some of them were known by names which evoked their character – in Curious Naturalists (1957:198) he even explained the process by which this was done:

> The first thing to do was to get to know individual birds, so that they could be recognized even after prolonged absence. With other birds, one

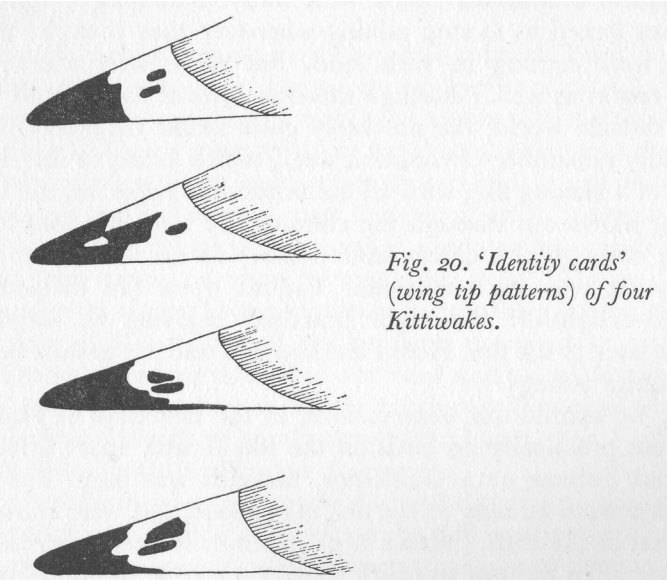


Fig. 20. 'Identity cards' (wing tip patterns) of four Kittiwakes.

[image 3] would do this by capturing them and marking them, for instance with coloured rings on the legs. But catching adult Kittiwakes on any scale was not so easy. We might have tried it but at best would have had very meagre results even after spending considerable time and energy on it.

Mrs Cullen found a much better way: she noticed that the pattern of black dots on the wing tips differed considerably from bird to bird and, after some practice, she could recognize a number of them by these 'identity cards'. Soon she found a good lookout post opposite a cliff inhabited by about 30 pairs of Kittiwakes. Because she was sitting there quietly day after day the birds soon got used to her and finally ignored her altogether. Her only equipment, apart from field glasses and note–book, was a chart with the drawings of the wing–tip patterns of those birds she had become personally acquainted with. (Tinbergen 1957:198).

Once the observer had become acquainted with individual birds (an interesting word choice in itself as the process of *acquainting* oneself being very different to, for example, purely *recognising* individual birds), those with specific characters become the subject of further observation, and clearly some speculation amongst the observers. Tinbergen was quite happy to use names for birds even where it was not his own choice to name them, as was possibly the case with another bird called

'Cleopatra'.[74]

To add a Cleopatra to a Casanova, aside from the somewhat mixed historical metaphor, certainly shows willingness to attribute human characteristics or see them as a part of a familiar human drama. What I mean by character here is quite significant, firstly that birds were recognised as having individual behavioural tendencies, and secondly that birds were given names of historically famous personae, which served at the very least as a shorthand for some aspect of the way that they behaved. Casanova means romance, or at least an irresponsible lothario lifestyle. In naming a bird Casanova, all the meanings that come with that are applied to the bird in question. Viewing birds with this kind of character is clearly at the extreme end of the anthropomorphic spectrum. Not all names come with such intellectual baggage, and a brief check of Tinbergen's fieldnotes also throw up gulls named Ursula and Peter, not directly associated with such instantly recognisably identifiable icons. Nevertheless, that even these birds with less immediately identifiable characters merited names shows that the Tinbergians were comfortable in the field with ascribing otherwise human artefacts (names) to their subjects. The following passage suggests that such naming might also entail a degree of possessiveness on the part of the namer:

> An immature Herring Gull flies over. All gulls (3) in my neighbourhood cry, the shrill kerr[75] rather trembling or quavering, and others birds attack it in the air, a lovely sight, but how furious they are and how quickly the H.G.[76] gets out!

74 In the same passage in Curious Naturalists Tinbergen outlines the methods by which individual identification could occur, he also gives a throwaway vignette on a mis–attribution of a name, that did not fit well with the individual character of the bird as observed by his student Esther Cullen:

> All through the four seasons (she spent three entire seasons and part of a fourth summer) she found that many of the birds had individual peculiarities in behaviour as well as in their appearance. For instance, there was one pair which always built an unusually high nest; another bird, a female, was too shy to mate; although she kept visiting males through season after season, she was always too nervous to stay with any of them. (This bird was inadvertently named Cleopatra before her character was known.) (Tinbergen, 1957:197)

75 Kerr, this is one of Tinbergen's onomatopoeic descriptions of the sounds made by the particular birds he is observing.

76 H.G. stands for the herring gull.

> 5.49 again, what a commotion.
> 5.50 The young bird (Peter) arrives again on his station, bird 2 keeus.[77] Peter alights and chocks[78] as reaction to his left neighbour who also alights.
> 5.58 Again it picks up material, lays it sideways, three times, then, after 3–4 seconds it stands up and shifts the eggs.
> After a minute it builds again 3 times in 5 seconds, but now it remains sitting, no shifting.
> The tide is high, about a foot above the nest, a bird left is bringing in long strands of nest material while its mate is on our nest. My bird cries out and low int. forw displ.[79] when it flies over, I see it 3 times. The tide is falling again however, (when came we had to wade well above knees).
> Tinbergen, (16 May 1951, MS.Eng.e.2749)

Here his description includes not just the naming and identification of one young gull as Peter; it also includes the description of "my bird" crying out, in one particular display (the low intensity forward display) as it flies over 'their nest'. There is a sense in the way he writes this paragraph of ownership of the birds, and their products– in this case by talking about 'our nest'.

The final bird to mention is Ursula (the origin of whose name is not explained), not least because she is not observed by Tinbergen directly, or by Esther Cullen, so it is clear from this that names of birds were passed around the group. Perhaps this suggests why birds with easily observable unusual or unique behavioural characters may have been given such evocative names, as they would be the most identifiable by other members of the group, and possibly also the easiest to call to mind. For example in this passage one of Tinbergen's students, J. Mike Cullen (husband of the aforementioned Esther Cullen), passes on some observations on a blackbacked gull he was watching that they had named Ursula:

77 This is another of the onomatopoeic descriptions of the sounds made by the bird.
78 Chocking is a classic Tinbergian referent, it is a forward posture combined with shrill noise, which he identifies frequently in bird behaviour.
79 "low int. forw displ." is Tinbergen's fieldnote abbreviation for the behaviour he called low intensity forward display.

> Mike told: miserable ill Greater Blackback "Ursula" standing near food, two first rate Herring Gulls nearby were frightened and did not dare take. Mere size might prevent crossbreeding between diff species of larger larus[80] groups.
> Tinbergen, (28th April 1954, MS.Eng.d.2387.B.16)

The remarkable thing here is the clear crossover between scientific hypothesis and what amounts to gossip. At second hand Tinbergen is being informed of one of the gulls being 'miserable ill' in that wonderfully evocative phrasing, at the same moment however, one further observation and hypothesis are added. Firstly Mike told him that even two 'first rate' herring gulls were too 'frightened' to try and steal the larger bird's food. The next sentence is a clear hypothesis about breeding and speciation: 'Mere size might prevent crossbreeding between diff species of larger larus groups.' Whether it came from Mike directly, or whether it was Tinbergen's own speculation, that it follows from the previous observation of the 'miserable ill' Ursula is evident. It intuitively follows– if herring gulls are too frightened to steal food from greater blackbacks, even those which are ill, perhaps their larger size is an issue that prevents crossbreeding too. Note too that the choice of the words describing the behaviour of the unnamed herring gulls is *frightened*, which should immediately recall my earlier discussion about Tinbergen's comfort with using anthropomorphic terms in fieldwork, even, in fact, in discussions with his students.

Tinbergen's anthropomorphism, then, was something that was pervasive in the field – he could comfortably use these terms in discussions he recorded with his students – and yet publicly he retained an image as the most objective and objectivist of observers. This idea of Tinbergen as an anthropomorphist or subjectivist is a difficult notion to accept as it runs against much of the standard image of Tinbergen and his school that I explained in the introduction to this chapter. The fieldnotes that I have outlined here are compelling evidence that this was the case regardless of the image

80 *Larus* is the genus for Gull, to which both the herring gull and blackbacked gull belong. Tinbergen mentions that Ursula is a greater blackbacked gull, which are larger than the herring gulls who are afraid of her. The greater blackbacked gull's Latin binominal is *Larus marinus;* the herring gull's is *Larus argentatus*.

he tried to convey to the public. Indeed it suggests that if ethology truly did need to be free of subjectivism and anthropomorphism to become a mature science, as he stated so often, then one person who needed to heed that lesson was Tinbergen himself.

Conclusion: Tinbergen's own Ethology

Tinbergen wanted to create an objective science of ethology, built upon professional scientific observers. More than that, and contra Crist's assertion that the Tinbergen was the mechanist par excellence, I showed that much of their work was practically done by trying to see the world from the gull's point of view (subjectivism). Furthermore, I showed that Tinbergen frequently strayed into anthropomorphism too, making use of a large range of human social terms and even ascribing human characteristics or personae to the gulls he and/or his students were studying.

My case study for this was the tale of Casanova in which perhaps all the rules of mechanomorphism are utterly ignored. This case study suggested that, far from the purely objective processes that Crist's work suggests Tinbergen must have been engaged with, quite different methods were at work. Firstly the character of the bird as an individual was considered, and then named in honour of one of the great figures of western literature, and a true cultural touchstone, then as now. De–individuation was a central platform of the mechanomorphic assertions, as seeing the birds as individuals with their own characters is not easily compatible with a view of them as behavioural automata. Secondly the idea of social drama was introduced, both in the observation and in the telling of the story, with Tinbergen's observations written with pace and entertainment, and with a real sense of the life of the birds again, they were social and behaving beings rather than automata. The social drama even extended to include the observers – so often written out of the third–person impersonal prose of the scientific publications of the Tinbergians – as they cheered on the exploits of the 'wronged' gull, and showed themselves to be engaged with the lives of the birds, including the less iconically named Ursula and Peter, whom they

were studying.

Tinbergen's fieldnotes therefore give us a route into his own ways of being Tinbergian in the field. This is important because it shows us a very different, but also a more complete picture of Tinbergen than has been available previously. Until the fieldnotes were examined, it seems to have been taken, almost on trust, that Tinbergen was working in the way that he told the world he was working. However, the picture is certainly more complex, as there is an intuitive, anthropomorphic side to his observations, which once revealed helps us to grasp exactly how it was possible for him to get a sense of what was significant as stimuli for the birds he was studying, before any serious experimentation had been undertaken. Indeed, the role that anthropomorphic thinking played in identifying possible hypotheses makes it for the atheist Tinbergen, a true deus ex machina.

Chapter Two: Tinbergian early years: the field

Introduction

The Tinbergians in the field were not merely engaged in the passive observation of nature. Instead they had the practical intent of systematic analysis in order to better understand the behaviours that they observed. Tinbergen had a wider ideal as well, in that he wanted his students to have a wide grasp of natural history, and of their place in the traditions associated with what was a well established discipline even in that period. Tinbergen had a specific and systematised way that he felt behaviours should be observed in order that the observations be sound as far as possible. This observation system was a difficult thing to follow in the field, and as we saw in the previous chapter Tinbergen often made use of both subjectivism and anthropomorphic thinking in order to circumvent these difficulties. The system that Tinbergen was trying to build was a modified form of Konrad Lorenz's idea of creating a *comparative anatomy of behaviour*. However where anatomists can easily cut up their animal subjects and study them in ever smaller parts, when applied to behaviour significant difficulties arise, particularly if the concern is for understanding natural or innate behaviour, as fleeting actions and movements cannot be recorded in the same way as the properties of an organ or a tissue. In addition, as the Tinbergians were committed to understanding natural behaviour they sought to intervene as little as possible in the lives of the animals they were observing. This contrasts very strongly with the interventionist approach common to the vigorous Behaviorist community which was particularly strong in America.

Tinbergen's background was considered in the previous chapter, as was its influence over his work, through his great affection for and appreciation of the animals he was studying, and this in spite of his noted public distrust of all of these things. We will see in this chapter that the kind of background that Tinbergen had was characteristic of a large number of both his students and other ethologists, and this certainly fed into the kind of science that ethology, at least in its early years, became.

This chapter then will look at the background to Tinbergen's students and his contemporaries, before considering the work of two individual Tinbergians in the field, focusing upon the methods and methodology they employed. To begin with I will look at the backgrounds that ethologists share, particularly focusing on those who became Tinbergians, but highlighting commonalities that ran across the discipline as well. In the second section I will investigate the empirical work of two of Tinbergen's earliest students, Robert Hinde and Martin Moynihan, in order to show two different ways that his students' work related to his ideas and methods. This investigation of his students' work will be the theme for the remainder of the thesis because their changing topics and methods do represent a good window on what was current practice by the Tinbergians at the various times they were working.

Section 1: "Ethologists are Scientists who love the animals they use in their research"[81]

The quotation above, attributed to R.F. Ewer, neatly captures something that ethologists recognised about themselves as a unique group, and it undoubtedly was linked to their lives as field amateurs. Amateur backgrounds, as I will demonstrate in this section, were the norm for early ethologists, a point recognised even by W.H. Thorpe, in his history of the discipline, (1979:66). Tinbergen was an amateur and a field man, and his time in the field pre–dated his formal biological training. Both Röell (2000) and Kruuk (2003) highlight his early membership of the NJN, the Dutch organisation for young naturalists. This early interest in, and affection for, nature was a characteristic of field naturalists of the period and was something which Tinbergen sought to reinforce in his own students.[82] I say *reinforce* specifically,

81 This is a quote attributed to R.F. Ewer by Eckhard Hess (1985:158). Ewer was an ethologist who studied large carnivorous mammals (see Ewer, 1973). She also wrote a general introduction to mammal ethology (Ewer, 1968). The attribution of this quote by Hess is unreferenced in his original usage, as I have not found it elsewhere in Ewer's writings I shall have to leave it as merely attributed by her by Eckhard Hess.

82 It was also a background that Tinbergen felt had played a key role in beginning the science of ethology in the years before the professional science was thoroughly established. In 'On the aims and Methods of Ethology' his most famous paper, which I discuss in chapter 4, he noted that early ethologists had been 'either field naturalists or zoo–men' (Tinbergen, 1963:411), and this was what had lent their interests to the field of behaviour: 'they were personally acquainted with an

because though it may not have been a stated necessary requirement to have been an amateur naturalist previously, it was a background shared by virtually all ethologists.

A youth interest in wildlife, and in birds specifically is a common feature of the overwhelming number of students of animal behaviour, Burkhardt even suggests it was near universal.[83] My prosopography on the autobiographies of the leading ethologists demonstrates that virtually all claim to have been fascinated, in love with, or captivated by nature, natural history, and specifically animals, from a very young age. For example, checking through Donald A. Dewsbury's Studying Animal Behavior: Autobiographies of the Founders (1985), the leading names of animal behaviour proclaim an early fascination with natural history and with animals with striking frequency.[84] Only two of the nineteen leading researchers on animal behaviour do not claim a passionate early interest, both of them Behaviorists.[85] One ethologist, Eckhard Hess,[86] felt he had identified a curious behavioural quirk common to the childhoods of many ethologists, which he felt identified those people likely to become ethologists:

> Konrad Lorenz once said that all of the ethologists he knew carried out this activity. I do not refer to the casual bringing home of some accidentally found frog or lizard, but rather the taking on of a

overwhelming variety of puzzling behaviour patterns which were simply not mentioned in behaviour textbooks.' (Tinbergen, 1963:411).

83 W.H. Thorpe in his reminiscences on the history of ethology: Origins and Rise of Ethology, even remarked upon early amateur interest in animals being the established pattern (1979:66). The rather haphazard nature of the book though, relying on reminiscence more than evidence of research, means that any quotes from there should be handled with care. Richard Burkhardt in his Patterns of Behaviour (2005) makes much the same observation 'This childhood fascination with animals… [was] virtually universal among the ethologists of the twentieth century.' (Burkhardt, 2005:132).

84 The biologists whose autobiographies were included in the book were: G.P. Baerends, V.G. Dethrone I. Eibl–Eibestfeldt, J. Langworthy Fuller, D.R. Griffin, H. Hediger, E.H. Hess, R.A.Hinde, A. King, P. Leyhausen, K. Lorenz, P. Marler, J. Maynard Smith, C.P. Richter, J.P. Scott, N. Tinbergen, E.O. Wilson, V.C. Wynne–Edwards.

85 The first person not to claim early interest was John Langworthy Fuller, who was interested in laboratory analysis of behaviour, specifically in domesticated dogs, and later on the laboratory mice, (Fuller, 1985:93–118). The other figure was Curt P. Richter, who came straight out of John B. Watson's Behavioralist laboratory and devoted a lifetime to a Behavioralist study of white laboratory mice.

86 Hess, although not trained by Tinbergen or Lorenz, was a German ethologist who was profoundly influenced by them. He directly acknowledge his debt both to Lorenz's early ideas, and to Tinbergen's Study of Instinct (1951) (see Hess, 1985:188).

> responsibility for providing an environment suitable for that particular animal and seeing to it that normal activities could take place in such a period of confinement. I distinctly remember that if these conditions could not be met, my animals were returned to the wild. I mention this aspect of my early life because I feel it has something to do with the nature of the kind of research that I have carried out over these years. It clearly supports the seemingly frivolous definition of the late R.F. Ewer, "Ethologists are scientists who love the animals which they use in their research." The long and short of it is that I have designed my research to avoid cutting up the object of study. Clearly this has its advantages and disadvantages. It is, however, interesting to note that the two students of mine who are clearly identifiable as ethologists, both cared for animals in their youth, neither cuts up the animals they use in their research, and both continue their work in the analysis of the behaviour of the complete organism in its environment. (Hess, 1985:183).

Hess's identification of the childhood interest and care for animals that he found as common ground with other ethologists is interesting, but more significant is the way that he feels this early affection for and interest in animals was what motivated him to do his ethological research in a way that avoided causing the animal studied any harm. This is a common feature of his work, and one that extends to his students, as he believes that they too chose not to injure animals in order to understand them. The informal observations by Hess, Lorenz and Ewer included in the passage above indicate that many ethologists recognised that their interest in animal behaviour far pre–dated their achieving the scientific study of it as professional scientists. Ewer's definition, even if intended frivolously, captures an essential aspect of the unique relationship between observer and animal in ethology: namely they drew aesthetic or emotional pleasure from animals years before they studied them as scientists. As Kruuk (2003:14–51) describes, this was true of Niko Tinbergen through his involvement in the NJN (Youth Organised for Nature Study)[87] a background Kruuk himself shares with Tinbergen (2003:29), along with many of the Dutch ethologists

87 In the original Dutch the title of the organisation is *Nederlandse Jeugdbond voor Natuurstudie.* Kruuk, (2003:28) loosely translates this as the 'Dutch Youth League for Nature Study.'

(c.f. Röell, 2000).[88]

Kruuk's observation that many ethologists had amateur backgrounds, and amateurs, particularly amateur ornithologists played a key role in the origins of ethology is backed up by Lorenz (1950:234), who noted that along with the world's professional zoologists such as the American C.O. Whitman, the German O. Heinroth, and the Dutchman J. Verwey, two *amateurs* also contributed important observations to innate behaviour studies: H. Eliot Howard and Edmund Selous. These two early twentieth century pioneers were both British '*bird lovers'* (ibid. emphasis in original) but were also crucial early field observers of animal behaviour. The personal history of many later British ethologists, for example Aubrey Manning, one of Tinbergen's earliest Oxford D.Phil. students, also share this common root for their interest in biology and animal behaviour, that of childhood or amateur ornithology:

> I came into biology along a route that is very well trodden in Britain– as a schoolboy I was a fanatical ornithologist. I was born in 1930 and brought up on the Surrey/Berkshire boundary, about twenty miles west of London– a region of brick houses, birch and pine heathlands with rhododendron. During World War II it was artificially peaceful, for the cars and aeroplanes that now dominated this overdeveloped, overpopulated landscape were blissfully absent. (Manning, 1985:289).

88 Röell suggests that early interest were common amongst Dutch ethologists often extending to very young childhood. (See Röell, 2000). For a critical review of Röell's work see Dehue (1997), though her review refers to the Dutch original rather than the English translation. However Kruuk notes an interesting feature of NJN amateurs in comparison with their British counterparts:

> Many people developed an interest as general naturalists, enthralled by the rich Dutch countryside that contrasted with their urban experience. Such a general interest in all animals and plants is still there. I see a clear contrast with for example, Britain, where many more people with a biological interest tend to be more specialized: they are ornithologists, or botanists, or entomologists, to the exclusion of interests in other aspects of nature. Niko in his later years was mostly a bird man, but with this Dutch background he was also keenly interested in and knowledgeable about plants, insects, and mammals. (Kruuk, 2003:28)

Quite why Dutch amateur naturalists became generalists and British amateurs became specialists is a difficult question to answer, and one which ethologists themselves speculated on without conclusion . Thorpe (1979:116) mentions that Tinbergen had observed to him that British students who could have become ethologists tended to become ecologists, and even suggests that those Americans who may have become ethologists under other (presumably continental European residence) conditions became Behaviorists. Neither Thorpe nor Tinbergen can explain this, nor, I am obliged to admit, can I. The reasons for this may well have been at the macrocultural level, well beyond the scope of this study.

Manning is far from the only anglophone Tinbergian to arrive at animal behaviour through this route. Robert Hinde, Tinbergen's very first Oxford D.Phil. student had a similar childhood interest in ornithology which motivated him to study animal behaviour. He too describes how this arose:

> My father was a family doctor with some specialization in obstetrics and a mild interest in natural history. Most of my education was at Oundle, and English boarding school with an excellent tradition of natural history. I was fortunate enough to come under the influence of an ex–Indian Army major who had turned from shooting tigers to collecting butterflies when he was not teaching boys engineering: Ian Hepburn, a remarkable Housemaster who taught me chemistry but who also and more importantly encouraged me in bird–watching and collecting beetles; Kenneth Fisher, a passionately ornithological headmaster who used often to take boys out bird–watching on Sundays; his son, James Fisher,[89] a broadcaster and ornithologist… So I was not short of figures with whom to identify. (Hinde, 1986:193).

Extending the anglophone web further, Martin Moynihan, the American who was also an early Tinbergen student, had an early interest in birdwatching that far pre–dated his arrival in Tinbergen's group. This is evident in the following correspondence with Ernst Mayr,[90] where Moynihan asks if he knew of any jobs that would be available for someone with an interest in ornithology, prior to his arriving at Princeton College for undergraduate study:

> I have tried recently to get a temporary job here in the Buffalo Museum of Natural History, but, as I expected, they are full up. I wonder whether you

89 That Hinde here mentions James Fisher is a reminder of how small the ornithological community was before the Second World War in Britain. Fisher was a close friend of the zoologist and modern synthesis contributor Julian Huxley, who was in his turn a great inspiration for the ethologists of the mid twentieth century. Fisher even became a part of the publishing team for the New Naturalist books after the Second World War in which Tinbergen published his Herring Gulls World, (1953).

90 Moynihan had previously encountered Mayr when the former had been a high–school age volunteer assigned to Mayr at the American Museum of Natural History, New York (Moynihan to Mayr, January 19th, 1952).

> would know of any sort of job connected with ornithology that I might apply for. I would very much like to be doing something worth while before I go back to college, instead of just wasting my time, as I have wasted enough time in the army already. (Moynihan to Mayr, March 8th 1948).

Mayr was doubtful whether this would be likely, or even possible, but he dutifully replied giving Moynihan the suggestion of the Fisheries and Wildlife service:

> I hope there will be no further interruption of your studies. You have lost enough time as is. I wish I could let you know of an opening for the summer, but unfortunately I don't know of any. The Museum here is hard up and is letting several people go. The Fish and Wildlife Service, which usually has lots of summer jobs, has had its appropriations cut and is therefore also reluctant to put on anybody new. Still, it might be worth trying. I don't know whether an out–door job would appeal to you. They are doing a lot of work at the present time in connection with the banding of ducks. And with censusing them in their breeding grounds. (Mayr to Moynihan, March 22nd 1948)

This began a lengthy correspondence, the already great evolutionist and systematist advising the young undergraduate on careers and opportunities, while Moynihan kept sending Mayr questions about potential career paths.[91] Moynihan once asked whether Mayr thought his artwork (pen and ink drawings of birds, that later were incorporated in many of the Tinbergianss famous works) was good enough for him to consider as a career.[92] Following this his interests shifted back to the purely ornithological, and so he once again wrote to Mayr:

91 The correspondence continued long after this, with letters forward and back for at least four decades, see the Ernst Mayr archive.

92 The letters concerning Moynihan's bird art are Moynihan to Mayr January 5th 1949, and Mayr to Moynihan, January 10th 1949. Moynihan's pen and ink drawings can be found, for example in Tinbergen (1958b) Moynihan is acknowledged in 3 of the diagrams of bird behaviour. However many of the others bear what I can only describe as 'striking similarities' to Moynihan's own pen and ink drawings, so his influence is demonstrated across the publication record of the Tinbergians.

> As I seem to be well into my senior year of college, I am now beginning to make some plans about Graduate School. I wonder whether you could tell me which schools in the East you would consider the best for someone hoping to do graduate work in Zoology, especially Ornithology. Your opinion on this subject would be of great value to me as I don't seem to be able to get any definite information down here. I hope that this will not cause you too much trouble. (Moynihan to Mayr, October 22nd 1949)

Gracious as ever, Mayr took time to dispense further advice in Moynihan's direction, suggesting caution in his choice of graduate college, as ornithology could be narrowing his choice both of university and of sub–discipline of biology.

> I shall be glad to give you advice on the school to be chosen by you for your graduate work. However, it will first be necessary for me to know a little about your plans. You now have been in college long enough to have formed a rough idea of your intended life work. Frankly speaking, if you are not terrifically enthusiastic about birds I would not, if I were you, choose a school where the emphasis is placed on ornithology. You may change your mind and then you may not be too well off. At the present time there is not a single school in the east that teaches ornithology that I can recommend. There are two in the middle west, namely Michigan and Wisconsin, and Wisconsin is the better of the two. In the far west there is, of course, California which is perhaps the best of all of them.
>
> Please tell me what particular aspect of ornithology attracts you most and what exactly you plan to do after you have obtained your degree. Also please tell me what other aspects of biology interest you most. I can make my further inquiries. (Mayr to Moynihan, October 25th, 1949)

Mayr's obvious interest in Moynihan is shown in the time and energy he devotes in giving his frequent replies to his young supplicant. His concern is that as Moynihan

decides to attempt a career in biology, he does not fall into the trap of narrowing his interests at the risk that they could change, leaving Moynihan stranded at a research institution which has a reputation and an interest only in ornithology. Moynihan however, though his interests were reasonably broad, was still set upon ornithology as a part of natural history, rather than any other part of biology:

> I am awfully sorry not to have answered your last letter before now but I have been very busy with a succession of tests. I greatly appreciate your suggestions about Graduate Schools. I have written to the three schools you mentioned asking for catalogues, admission blanks etc. I am also applying for a Fulbright Fellowship to study in England.
>
> I have definitely decided to go on in Biology. My chief fields of interest are in Natural History, Comparative Anatomy, and related subjects. I am largely, but not exclusively, interested in these in their application to Ornithology. I therefore want to continue my studies in a school where considerable emphasis is placed on these subjects. I certainly do not want to get in one where Biochemistry is emphasized.
>
> Thank you again for the trouble you have taken on my behalf. (Moynihan to Mayr, November 19th, 1949).

With that Moynihan made his decision, resulting in his taking up an offer to study under Niko Tinbergen in Oxford. Once again it is the pre–existing love of ornithology that sends a student in the direction of ethology, with the result that Moynihan became one of Tinbergen's early Oxford students.

Curiously, even with a relatively solid stream of potential students arriving from the massed ranks of amateur naturalists and amateur ornithologists, the early ethologists were not comfortable with the calibre and more particularly with the type of student that was arriving at their doors for instruction as postgraduates. This is shown in a reply to a letter from Tinbergen to Mayr. Although the initial letter it seems is lost to us, it is apparent from the content of Mayr's reply that it was complaining about the lack of interested and capable students with a broad enough sense of the natural

world, or a sense of natural history, as opposed to narrow individual disciplines:

> You made several acute observations in your letter about students and the development of our science. We, in this country, are very much up against the same thing. Several of the natural history societies no longer get any young members. It happens more and more often that young colleagues admit that they were not interested in biology until after entering college. Obviously their research interests will be totally different from those who virtually start life as naturalists. I don't know where this development will lead to, but it is a vicious circle which gets worse every year. The main cause of it in this country is the teaching of biology at the level of what in this country is called the high–school (equals gymnasium in Europe). Most of these high–school biologists do not know one animal from another and teach all about genes and enzymes from books. There is none of the enthusiasm or concreteness that should be in the teaching at this level. I don't know where it will lead to. We have entire universities, also, where zoology is no longer taught, but only special aspects of it, like cytology, genetics, embryology, and physiology. The students lose completely the feeling for the living animal. (Mayr to Tinbergen, December 15th, 1953)

The mark of an ethologist has been early interest in and affection for animals as living beings – scientists who love their animals – in Ewer's terms. Nothing then would worry ethologists more than the idea that this youthful interest and affection for animals was being curtailed, whether by the actions of narrow curriculum teaching, or by some other unrecognised force.

Section 2: Two of Tinbergen's earliest students, Hinde and Moynihan

Tinbergen's early students were an industrious group, churning out publication after

publication, and thesis after thesis, and almost without exception in the early period they chose to stay close to the ideational frameworks that Tinbergen had developed. Tinbergen though was certainly not a rigidly orthodox thinker who ruthlessly disciplined his students either in terms of their theoretical or even their methodological approaches.[93] As a consequence of this his students' work is quite varied, both in terms of the animals studied and also the methods they employed. Two of his earliest students were Robert Hinde,[94] later Regius Professor of Zoology at Cambridge and Martin Moynihan, later director of the Smithsonian Tropical Research Institute. They took to the Tinbergian approach in very different ways, Hinde being more prepared to make use of technological aids to observation, for example, than Moynihan, who preferred to rely on his own direct observations. In the following sections I will explore their work in turn, first looking at Hinde's, as he arrived first, and then turning to examine Moynihan's work.

Section 2.1 Hinde's way out of the woods

Although Robert Hinde was not officially one of Tinbergen's students, being registered under David Lack in the Edward Grey Institute for Ornithology (universally known as the EGI), Hinde himself credited Tinbergen's non–official supervision as being the single most important influence over his work. Tinbergen had arrived at Oxford just after Hinde, who had himself only just finished his wartime national service and been decommissioned, after which he immediately began work on his D.Phil. and Tinbergen did much of the practical supervision of Hinde's thesis, and left an enormous imprint on Hinde and his work: 'the most important at that time was Niko Tinbergen, who taught me how to analyze behaviour

93 Tinbergen hints at relative openness to his students taking varied approaches. For example he talks about a 'keen' visiting student who wanted to study sticklebacks focussing only on one small aspect of their behaviour rather than by understanding their ethogram as a whole, Tinbergen allowed him to do this, although with reservations (Tinbergen, 1953a: 130).

94 Hinde credits Tinbergen directly with his development as a biologist, even though he was in the presence of some of the foremost ornithological minds of the era:

> David Lack imbued my behavioural observations with an ecological slant – and I profited too from the proximity of Charles Elton, Dennis Chitty, and Mick Southern at the Bureau of Animal Populations, next door to the Edward Grey Institute. But the most important influence on me at that time was Niko Tinbergen, who taught me how to analyze behavior – and it was his lessons especially that I carried with me to Madingley. (Hinde, 1985: 194)

– and it was his lessons especially that I carried with me to Madingley.'[95] (Hinde, 1985:194) Hinde chose the great tit (*Parus major*) as his study animal, a very different animal to study than the gulls that Tinbergen had observed in the Netherlands. Great tits are a woodland species, which necessitates a different observer style, as they can dart in and out of trees or bushes and thus hide much more easily than gulls on dunes. Hinde did his observation in Wytham Woods in rural Oxfordshire, making use of the nascent Oxford University field station there.

Hinde's methods are related but different to those that Tinbergen outlined above and in this Hinde is especially interesting precisely because his position is somewhat transitional, as he began his research before the school began, and therefore incorporated other techniques from other areas of animal behaviour and ornithology. Hinde's work is noteworthy for his use of more interventionist techniques and technologies than would be found in the classical period of the Tinbergians, to which Moynihan belonged. Hinde, for example, bases much of his observations on a range of ornithological techniques, first trapping the birds, then ringing them, and then setting up automatic recorders to monitor entry and exit of the nests.[96] Hinde though

95 By 'Madingley' Hinde is referring to the Subdepartment of Animal Behaviour at Cambridge University, where Hinde spent the rest of his career.

96 Hinde described the methods he used, and his description shows that he was very comfortable to use a variety of both of observation styles and technologies. His level of intervention in the lives of his birds is quite a lot higher than Tinbergians' of the classic era of the school in the 1950s. He trapped birds in order to ring them, as ringing was a tool for identifying individual birds. In detail here is his list of field techniques:

SECTION 2. TECHNIQUES.

A. Trapping.

Trapping was carried out from November to March each winter. A variety of traps were used, but the most successful consisted of ¼ inch wire netting over an 18– inch cube wire frame. The birds entered through a semi–circular funnel (8" long, and of a radius of 2½" decreasing to 1½") placed at ground level. A small door at one side served for removing the birds, and could be left open when the trap was not in use. The traps were baited with sheep's fat. Much of the success of the trapping depended on adequate pre–baiting: the traps were left open and baited, with more fat hanging up nearby, at all times when trapping was not in progress.

B. Ringing.

All birds trapped were marked with a numbered Aluminium British Museum ring on one leg, and with two or three coloured rings on the other. The coloured rings enabled individuals to be distinguished at distances of up to about thirty yards. Some of the birds had been marked previously by J.A. Gibb, so that some of their previous history was known.

C. Age and Sex of Trapped Birds.

It is not always possible to distinguish the age of Parus spp. in the field… [*This is a whole segment on identifying sex differences, mostly done by wing length, and includes a section on the ratios at which different sexed and aged birds were caught. While fascinating for those interested in the early history of ringing it is however, largely a side note for the purposes of my study.*]

does show considerable Tinbergian influences in his final D.Phil. Though they are perhaps more evident in his analysis than in his initial techniques (see footnotes below), the traces of Tinbergen's approaches are palpable. For example in his D.Phil. Hinde gives lengthy consideration to those behaviours involved in fighting over food (1951:37–45), but it is a complete mixture of observation styles and techniques, as is suggested by examining his sub–section headings:

(a) supplanting the attack;
(b) combat;
(c) stealing;
(d) head–up posture;
(e) wings–raised posture;
(f) head–forward posture;
(g) flying off with food;
(h) avoiding behaviour;
(i) re–entering the flock;
(j) "individual distance". (all from Hinde, 1951 37–45)

Hinde's description is structurally complex in that a range of different analytical behavioural objects are presented. Looking at this list (d), (e) and (f) are unmistakeably Tinbergian, describing 'clearly recognizable postures' with names that do not imply interpretation (as Tinbergen set out above).[97] The other subheadings, including topics like 'combat' and 're–entering the flock' and especially 'stealing' do make explicit claims about the function of the behaviour in the title that describes it. If we examine Hinde's description 'flying off with food', it is as much a consideration of the function of the behaviour as it is a description, something that

D. The Automatic Recorder.

The rhythm of various nesting activities were studied by means of a automatic recorder. A trigger was placed in the entrance to the nest box in such a way that the bird made one contact every time that it entered, and another each time it left. Each contact operated a pencil writing on a revolving drum. The apparatus was designed and constructed by J.A. Gibb. (Hinde, 1951:8–10 Italics inserted by me)

97 As Tinbergen's abstemious admonition post–dates Hinde's thesis (written in 1951), it cannot in that instance have been the cause. It may have been that Tinbergen chose to reiterate his methods and analyses in response to the way that Hinde had mixed together his own approaches and analyses with those of EGI ornithologists, but this is only speculation.

contrasts with Moynihan's work, that we will look at in the next section, from a year or two later. Hinde then looks in more detail at the behaviour he labelled 'Flying off with food'. He begins with description, but moves quickly on:

> (g) Flying off with food
>
> When a tit finds a piece of food so big that it cannot be swallowed immediately, it flies off and eats it elsewhere. Nuts and beechmast are always dealt with in this way. The value of this behaviour to the individual may be that he can thereby open and eat his nut in a place where he is less exposed to being robbed by other birds. Sometimes many individuals from a flock carry their booty to the same bush; but even so they probably gain some immunity from attack, as the neighbouring birds are feeding, not searching for food. The carrying away of the food may also be of value in that the bird opens its nut in a position where it is less exposed to predators.
>
> The birds readily become conditioned to carrying their food to a particular bush: at houses where the tits habitually open the milk bottles and carry away the stoppers, piles of stoppers are found behind their favourite bushes.
>
> In periods of great food abundance tits sometimes carry off food, and then leave it without eating it and return for more. Blue, Coal and Marsh Tits were often seen doing this during the heavy beechmast crop of 1948. The Marsh Tits usually flew down to the ground with the nut and pushed it into the moss: the same individual would return repeatedly to the same area, but not to the same spot: so that in a few minutes several nuts would be deposited within an area of a few square yards. The Coal and Blue Tits usually pushed the nuts into the cracks in bark or into the holes in the centre of elder boughs. Similar behaviour has been recorded previously in Great and Willow Tits, and also in P. bicolor,[98] as well as in the species noted above (Fatio and Studer, 1889; Lewis, 1923; Astley,

98 *Parus bicolor* was the Latin name for the Tufted Titmouse, a common American member of the Tit family at the time Hinde was writing. It has since been reclassified as *Baeolophus bicolour*, as *P. bicolor* has become the standard abbreviation for Dogweed.

> 1923; Hibbert–Ware 1929; Forbush, 1929; Morley, 1942; Owen, 1945; Bent, 1946; Southern, 1946; Richards, 1949)[99]. In all cases for which adequate data were given, food was temporarily superabundant, and each particle of food was carried to a slightly different place, being usually pushed into a crevice in a stump or behind ivy. It seems unlikely that the bird remembers later where it put each particle of food, but it may remember the general area, so that this is probably real food–storing behaviour. Certainly it is not merely a case of a behaviour pattern being cut short because part of the adequate stimulus (hunger) for the final act (actual eating) is missing. The chain is cut short before the food is opened, and in most cases the food is not merely dropped, but hidden. The behaviour forms so definite a pattern that it must have survival value. (Hinde, 1951:41–43)

Hinde here is definitely aiming to describe an observable behaviour of a qualitatively different character to, for instance, the 'wings–raised' posture. He does note that the behaviour has a definite pattern (in the last line of the extract), and uses this to justify the idea that it must therefore have a survival value, but it is a vastly more varied pattern than the kind of muscle movement level of analysis that Tinbergen advocated. The large pattern of behaviour which falls under the rubric of ‘flying off with food’ involves a range of actions and movements that are vastly greater than those described by the term ‘head–up posture’. What is more, there is an important assumption of function in the title of the behavioural description ‘flying off with food’ that is not present in ‘head–up posture’, in that it is a title which suggests a purposeful behavioural chain. This is clear because Hinde's assumption is that the purpose of the behaviour is to take foodstuffs somewhere. That makes a great deal of sense in the situations that he stipulates, but is by no means close to the strictures that Tinbergen's methods argue for. Hinde's discussion is a far cry from what would, following Tinbergen’s own discussion of methods, come to be seen as the Tinbergian ideal of pure description shorn of speculation on function or cause.

99 All of these studies are included in my bibliography as they were in Hinde’s original referencing. They represent a snapshot of the Paridae studies as Hinde encountered them.

There is in Hinde's writing a surprising breadth of engagement with research from outside the Tinbergians underlining Hinde's approach. This is found in the lengthy citation of previous studies of Tits, and also in his mentioning of conditioning, a subject more associated with Behaviorists; and of chain reactions, which is more characteristically Lorenzian than Tinbergian. These characteristics reflect the fact that Hinde was already at Oxford when Tinbergen arrived and so was subject to other interests, but also perhaps the fuzzier edges that are permitted before harder disciplinary boundaries (c.f. Clarke, 1998) are formed. Hinde's study then is very different to the ethogram ideal that would develop in the classic years of the Tinbergians, but it provides a valuable snapshot on what was happening when Tinbergen arrived – and also demonstrates different directions that Tinbergen might have taken early on – by, for example, focussing on survival value in the way that Hinde does here, and that would not recur as strongly until his 1960's eggshell studies, or even Dawkins' work. Another direction his school might have taken could have been to have made greater use of automatic recorders, or more intervention in the lives of their birds, such as by generalised use of ringing. Instead of this Tinbergen's students, particularly his field students followed another path, the one that he had set out himself, and the one that was most faithfully followed by his student Martin Moynihan.

Section 2.2 Moynihan's path through the dunes

Martin Moynihan, one of Tinbergen's earliest students, forms an interesting and contrasting pair with Hinde. Like Hinde, he arrived at Oxford after war service, though Moynihan's had been as an American GI in Korea. Like Hinde he also was an enthusiastic amateur ornithologist but when he arrived at Oxford he began studies on the blackheaded gull (*Larus ridibundus*), which is a classic ground–nesting gull, and one of the same genus to Tinbergen's own favoured herring gull, (*Larus argentatus*). Moynihan not only chose a closely related species to Tinbergen, he also very closely followed Tinbergen's methods. Whereas Hinde had enjoyed the relative freedom to observe many different types of behavioural object, from "combat, or "flying off with food", to Tinbergian observations of certain postures, Moynihan's work was much

more focussed, mostly following Tinbergen's strictures. Moynihan also chose to almost exclusively use direct observational methods, with most of his observations at his field site, though a few were made on aviary birds.[100] We can see the emphasis that he puts on direct observation in the methods discussion from his D.Phil.:

> 2. Methods.
>
> Most observations of the Black–headed Gull were made in the field, at three different gulleries, during the breeding season. Two complete seasons, and part of a third were spent at these breeding colonies. In 1951, observations were made at the gullery on Scolthead Island, Norfolk, from April 2 to July 15; while in 1952, work was done at another Norfolk gullery, Scoulton Mere, from March 2 to July 1. Supplementary studies were completed, during March and April of 1953, at Ravenglass in Cumberland.
>
> Field observations were generally made from hides. The gulls rapidly became accustomed to the presence of such structures; and they could thus be watched from very near.
>
> The behavior of some captive juvenile Black–headed Gulls was also briefly studied. These (nine) juveniles were placed in two small aviaries (11' x 3'6" x 4'9"), in the Department of Zoology at Oxford. They were kept during the late Summer and Autumn of 1951.
>
> Work on the Silver Gull was done in the Regent's Park Zoological Gardens, London. A number of these gulls inhabited a large flight aviary, along with a mixed assortment of other birds, (ibis, cormorants, sheathbills, herons, etc.). They were studied for short periods, at various times from January 1952 to April 1953.[101]

100Though he did also bring some chicks back to the laboratory in Oxford, but they do not appear influential in the progress of his D.Phil. account of his research. This bringing of the chicks to Oxford does present an interesting counterpoint to the ideal of the purely inductive or observatory description, and also to the image of the school as entirely field–based, but as ever, the world is more complex than the standard images. Moynihan only mentions it in his Abstract, as far as I can tell (Moynihan, 1954:iv).

101 Moynihan's research here might give the impression of very broad research, but checking the dates and times of the length of the research shows that the largest single aspect of his research time was in the field at Scoulton Mere or Ravenglass. Indeed there is nothing to suggest that his observations at the zoo were anything more than the briefest of visits, ibises for example, are very distant from the gull family, and do not even belong to the same biological genus, family, or order.

> The Little Gull, like the Black–headed Gull, was studied in the field. A little Gull colony in Friesland, the Netherlands, was observed for a few days in early May 1952 and 1953. (Moynihan, 1953:2–3)

Moynihan's D.Phil. is based on his own fieldwork, though he does mention that he also observed young birds in aviaries in Oxford, and comparative species in London Zoo, and in the field in the Netherlands.[102] Moynihan's research only used his own observations of behaviour, rather than the automatic recording of arrivals and visits that Hinde used. The quotation above demonstrates how central the idea of observation was for Moynihan, to the extent that though the section heading is "Methods," all we are informed of initially is when and where he made observations of blackheaded gulls. For Moynihan, *the way* to study birds in the wild is through pure observation, indeed the note is continued last paragraph where the words '*observed*' and '*studied*' are used almost as placeholders for each other.

There are two further points that we should take out of Moynihan's brief discussion of methods in the quotation above, both of which point directly to his Tinbergian heritage. Firstly, there is the extended period of time in the field, something he shares with Hinde who also spent a lengthy period employed in field research,[103] and also he is in accord with Tinbergen's own beliefs of the values of lengthy field study. The second dimension that should be noted which helps to place Moynihan as a fully fledged Tinbergian is in his use of comparison. This connects directly with the sections above where I have discussed the influence of comparative morphology on Tinbergen's early thinking. This is a second area in which his work shows distinct similarities with Hinde's, as Hinde's was a comparative study of the whole genus of the Paridae. Moynihan's central focus was the blackheaded gull, but as shown above in the list of other gulls that he observed there were explicit comparisons made with

102 Although there is the appearance in Moynihan's work of extraordinary breadth of comparison, this vanishes when you look at the dates he was at each research site for. There is a tremendous difference between a few days of study as was the case on the Dutch little gull colony, on the one hand and the intense breeding–season–long study of the blackheaded gull on the other, and these season–long studies provided the vast majority of the research observations which in turn form the data for most of analyses.

103 Hinde's was somewhat curtailed field period as his D.Phil. was allowed to be shorter than normal as he was a returning soldier, and managed to complete it in about two years. (Hinde, interview, 16th December 2005)

silver gulls and little gulls, as well as much more distantly related birds, such as the cormorants and herons. Furthermore Moynihan's whole study should be read in the context of Tinbergen's wider project, which he outlined to Mayr (and which I mentioned above) of building a set of comparable observations across many gull species, for which his own herring gull work would form the exemplar.

Moynihan's work does have noticeable differences from that of Hinde's, however, and the most apparent is in the reliance on non–interventionist direct observation that is suggested in Moynihan's approach to field observation. Hinde's work had differed from this in two ways, firstly his had not been solely direct observation, as he made use of automatic recorders as an auxiliary way of noting the movements of birds. Secondly Hinde had made use as a central tool of his research, of techniques of capture and ringing, though these were also intended as an aid to direct observation, as they were used to identify individual birds. Moynihan's research did not make use in any meaningful way of techniques auxiliary to observation, whether through the use of recorders or of ringing. Neither did the main bulk of his research make use of intervention in the lives of the birds under study. Whilst the automatic recorders and ringing are very much at the low end of the intervention scale, Moynihan's research sat even lower, relying almost entirely on observation to build his species's ethogram.

Moynihan's study is *the classic attempt at an ethogram*, and nothing except Tinbergen's own The Herring Gull's World (1953) even comes close to it in this early period.[104] This means that his work has incredibly high levels of observational detail, even for identifying what might seem a simple behaviour like "choking". This forms a very strong contrast with Hinde's work in the previous section in whose work the most detailed description of a single behaviour was for 'flying away with food' which I reproduced in full above. Most of Hinde's descriptions were therefore only a few paragraphs and there are no diagrams of the behaviours described. The contrary is true for Moynihan where no description is less than a few pages, and page sized diagrams are also always included. For example Moynihan goes to an exceptional

104Esther Cullen's famed work on kittiwake adaptations does come close to the ethogram, but her addition of evolutionary and ecological factors mean that it is a substantially different piece of work to Moynihan's, as we will see in chapter four.

length merely to describe the action of "choking," including using his own beautiful pen–and–ink drawings:

> (D) CHOKING.[105]
>
> (1). Description of Choking.
>
> Choking is the most elaborate, and rarest of the threat displays of the Black–headed Gull.
>
> The typical Choking Posture (see pl.7 [image 4]) is very distinctive. The body is strongly tilted forward and downward, so that the breast rests on or near the ground. The rear part of the body and the tail are raised up. The body as a whole forms an angle of about 75° with the ground. The belly feathers are conspicuously fluffed out. The mantle and scapular feathers seem always to be smoothed flat. The neck is moderately extended and strongly arched. The head and bill point downward; the bill often touching the ground. The carpal joints are held away from the body and the tail is often spread to a considerable extent. The legs are usually bent.
>
> It is not rare to see a Choking Posture in which the wings are raised and spread (see pl. 8, fig. A [image 5]). Sometimes the wings are held extended and motionless; sometimes they are flapped. The tail is then bent strongly upward and forward so that it approximates to the vertical.
>
> The sound made by a Choking Black–headed Gull is particularly interesting. This utterance has the quality suggested by the name given to the display. At high intensities it might be transcribed as "Kruh–kruh–kruh–kruh", "Kro–kro–kro–kro–krohoo," or "Krohr–krohr–krohr–krohr–krohr"; very rapidly and rhythmically repeated. There is something about this sound that suggests it is being produced
>
> [image inserted as 4] with considerable effort; as if it had to pass some obstruction in the bird's throat. Although low in pitch these sounds are penetrating.

105 Moynihan has a footnote at this point which I will reproduce: *The term Choking has been used by Nobel and Wurm (1943) to describe a similar behavior pattern in the Laughing Gull. The Choking Posture of the Black–headed Gull seems to be that posture called the Downward by Kirkman.* (Moynihan, 1954:60)

> Certain movements are associated with Choking. A gull often sits down momentarily, on its tarsal, while Choking. A Choking Gull may also turn around from side to side; sometimes making backward kicking movements like those of a gull scraping during nest–building. (Sometimes the bird merely moves its legs up and down alternately).
>
> As the call is uttered, the bird's head goes up and down in a pumping movement. The bill is slightly open. The tongue bone is depressed. This gives a rather swollen look to the lower part of the face. Now and then a Choking gull picks up twigs or blades of grass in its bill. I have even seen birds deposit such twigs, over their shoulders with a typical sideways nest–building movement. The raised feathers of the lower breast and belly go in and out rhythmically in close correlation with the Choking Call. In addition, the cloaca is sometimes rapidly opened and closed.
>
> The orientation of Choking is perhaps slightly unusual. Two gulls, Choking at one another, may face in any direction. Most frequently, however, they stand side by side, facing in the same direction. Two gulls, standing this way may bend their heads sideways, away from each other.
>
> [Image 5] (Moynihan, 1954:60–62)

The depth of observation here is apparent – consideration of function and causation are secondary if not tertiary tasks, the aim is to investigate and deliver a reliable description of the behaviour of 'choking'. Moynihan is writing to describe and define behaviours, rather than to analyse. It is worth bearing in mind when considering the whole extract that Moynihan is trying to describe a single posture and its variants. This is not, on the surface, a complex behavioural pattern or chain of the type that Hinde was describing with food movement to avoid stealing; on the contrary it is a single posture and is exactly the sort of description that Tinbergen had talked about in the 1952 notes on methods.

In addition to the length and level of detail discussed in the previous paragraph several further things emerge from this long excerpt: firstly, Moynihan's passage

contains two intricate line drawings; secondly there is throughout the piece a tone of studied mechanomorphism; thirdly there is the use of onomatopoeic descriptions of the sounds made in the behaviour; finally there is an implicit suggestion of comparison in his work. Each of these characteristics has a relationship with Moynihan's situation as a Tinbergian, but none of them is simple, and so I shall explain them hereafter. As someone whose talent as a bird artist nearly led him in that direction, as we saw in the previous chapter, it should be no surprise that Moynihan's thesis is filled with his own drawings. Following Moynihan's work, the diagrammatic depiction of behaviour became the norm in Tinbergen's student's theses, something that had not been the case when Hinde had produced his. We will discuss the Tinbergians diagrams in the next chapter, but it is important to note that their presence is only common after Moynihan's work.

Moynihan's mechanomorphic descriptions should not be a surprise to us as readers, as mechanomorphism was such a central aspect of Tinbergen's scientific writing strategy. It is clear that he wished to describe movement–by–movement the postures assumed by the gulls involved in choking, and in doing this he goes down to the level of describing where certain bones are such as the tarsals, and the jawbone, and feather postures, and this partially has the effect of reinforcing the mechanistic tone, as it obscures the bird as a whole behaving unit. This observation fits with Crist's (1999) work on mechanomorphic descriptions that I noted in the previous chapter, which was such a part of Tinbergian scientific writing. It also fits with the character of recording (in a written form) sound–by–sound the noises made by the gulls, in a manner very similar to the observations of their physical movements, both of which were seen as a part of their behaviour. Tinbergen himself had described in this onomatopoeic manner the sounds made by the related herring gulls while they were 'choking' (Tinbergen, 1953b: 60–61),[106] which should in turn remind us that

106Tinbergen's description of choking in the herring gull is too lengthy to reproduce in a footnote here, but one passage does merit closer attention at this point: 'The call sounds like “houh–houh–houh–houh...” Sometimes the birds also make scraping movements with the legs. The whole performance is rather similar to the actual making of a scrape (a nesting activity found in many birds besides gulls). Usually however, the actual scraping with the legs is omitted by gulls in a hostile situation.' (Tinbergen, 1953b: 60).
I think it is particularly interesting that not only does Tinbergen use onomatopoeic reproduction of the birds call, but also that he ends with 'usually however, the actual scraping...' Moynihan's unqualified use of the world 'unusually' seems to be closely aligned with this passage whether

Moynihan's passage here can be seen as a part of Tinbergen's own large *comparative* project. That at least part of Moynihan's orientation was comparative is suggested in the passage itself, where he states that 'the orientation of choking is slightly unusual,' a statement that cannot be purely self–referential, but rather an observation that necessitates comparisons. The logical comparison is with the other gulls that Tinbergen had himself studied, especially as he had previously stated that his aim was building ethograms for comparison.

In the next chapter of his thesis Moynihan turned from description to analysis. His analysis of the behaviour is also almost entirely qualitative rather than quantitative; about observing instances of certain behaviour patterns and classifying them as behavioural units, rather than applying statistical methods to them. Statistical methods were clearly something he felt was inappropriate to his data particularly as his data rested on a theory of 'drives.'[107] Drives were profoundly important analytical

consciously or not. It represents the original, to which Moynihan's implicit comparison is made.

107On the difficulty of statistical measurements of drives, which are essentially internal states, Moynihan is quite clear that the only possible solution is relative rather than absolute measurement:

> Something should be said about how I have measured these drives. Unfortunately, it has not yet been possible to measure them in an exact quantitative way. There are large practical difficulties in the way of such an attempt: the difficulty of presenting standard stimuli under more or less standard conditions in the field, etc. It is, however, quite feasible, and fairly easy, to get two independent sets of relative and approximate measurements. The strength of the attack and escape drives may be compared, with one another, in any particular threat display. This can be done by comparing the apparent vigor of the intention movements of the two drives in this display, by observing the orientation of the displaying animal, and by counting the frequency with which this particular display precedes (or mixes with) actual attack and escape. As a result, it is possible to say that, in any given threat pattern, the attack drive is very much stronger, or approximately equal, or very much weaker, than the escape drive.
>
> It also seems feasible to determine whether in any given threat pattern, both the activated drives are generally weaker or stronger than they are in any other particular threat display. This can be done, primarily, by observing specific conflict situations; (seeing whether certain disputes are prolonged, whether they are territorial, whether they are associated with non–hostile behavior patterns, whether they are interspersed by actual escape behavior and/or violent attacks, etc.). The various types of hostile encounter can thus be “graded”, according to the apparent intensity of the dispute. The frequency with which each threat patter usually occurs in each type of hostile situation is then of great value in determining the strength of the two drives. (Moynihan, 1954:78–79)

Moynihan clearly believed that relative measurement represented the solution to the problem of measuring drives. His solution is also interestingly an observer's solution, based on comparing the vigor of various different movements, rather than for example, trying to measure the internal brainwaves of the birds, or putting them into experimental situation in which they chose one option or another, in which the options represent outcomes to one drive or another. We should note therefore the extent to which he remained non–interventionist in the lives of the birds he was studying. His methods were a crucial point of choices, at which he ruled out intervention, and

tools for studies of animal behaviour in this era, and were central to the way that Tinbergians understood and analysed behaviour. The idea of the drive was complex, and involved multiple usage of the same word for distinctly different concepts, a point later noted by Hinde (1956:324–326), who identified at least three different though overlapping senses in which it was being used by Moynihan and Tinbergen. Hinde suggested that there had been a drift in usage by ethologists generally toward using 'drive' to describe 'all the causal factors influencing the behaviour, whether internal or external' (Hinde, 1956:326), however, he states that Moynihan used one meaning, and that was: "all causal factors other than those received through exteroreceptors.[108] Thus Moynihan defines it as 'specific readiness to respond to releasing stimuli'.[109]" (Ibid.) Moynihan's understanding of the term, with its emphasis on specific responses, is what underlies his analyses of his observations, whilst simultaneously providing those questions which interest him most. To follow on the 'choking' story, we can see that drives were both the explanation for certain behaviours, but also the reason why choking represented a phenomenon worth studying. He analyses choking relative to the context of its being performed, in order that he can see what drives may be being stimulated by the surroundings or surrounding birds. Here is his analysis:

> Choking is usually the rarest of the threat displays. It is almost always associated with certain definite conditions.
>
> Choking is particularly characteristic of prolonged disputes; both prolonged squabbles in which much actual fighting occurs and prolonged squabble in which little actual fighting occurs. It is, for instance, conspicuous that during many boundary disputes; e.g. when a pair of mated gulls, over a period of several days, try to "wedge" themselves into an area whose whole extent has previously been the territory of another pair. This display is, generally, more often seen during the incubation period, when the gulls are crowded together on small territories, than

thereby chose to work with observation, and thus develop a way for measuring drives which was purely observational. If we recall Tinbergen's writing on methods above, it is significant that Tinbergen himself recognised the difficulties posed by trying to measure and record intensities

108 Hinde never explicitly defines what he means by exteroreceptors, but I think it is reasonable to infer that he is meaning senses attuned to the world outside of the animal itself.

109 Hinde is referring to Moynihan's Blackheaded gull paper in Behaviour (Moynihan, 1953:58).

> during the pair–formation, when the gulls are rather more scattered. It tends to increase as the crowding increases.
>
> Choking is almost absent when gulls have congregated together in communal preening or feeding grounds. Prolonged disputes are also uncommon under these circumstances; but the other threat displays, and brief attacks, are not infrequent.
>
> All these facts indicate that both the attack and escape drives of a Choking gull are very high indeed.
>
> One problem remains. Is the attack or the escape drive the strongest in this display?
>
> Unfortunately, for purposes of clarity and nice clean–cut distinctions, either drive may, apparently, be preponderant. A gull may also Choke immediately before it charges to the attack. During a boundary dispute, one of the birds may advance steadily, Choking continually; while its opponent will as steadily retreat, also Choking continually. (Moynihan, 1954:78–80)

Moynihan begins here by identifying the key features of the context of choking behaviour. This is because he intended to use a system of 'relative and approximate measurements' (Moynihan, 1954:78) to understand the drives motivating the behaviour he is studying. The most important features governing the likelihood of the behaviour being exhibited as far as his analysis is concerned are: in prolonged disputes (between birds); in boundary of territory disputes; and during incubation rather than pair formation. These features are important for Moynihan because they relate to his intention to identify and measure the drives underlying the behaviour he is studying. The drives involved are something to do with either attack or retreat, though as he explains further along he could not ascertain which was more strongly activated.

To understand choking behaviour then, Moynihan is using a three part system, whereby firstly he seeks to understand which drives are stimulated, secondly to what extent, and finally to determine the most important drives involved in stimulating a

certain behaviour. Once again we can relate Moynihan's work to Tinbergen's methods writing, as the relative and approximate measurements that Moynihan is referring to bear a significant resemblance to the type of observations that Tinbergen described in his methods writing. Tinbergen's methods required that observers: 1) described 'clearly recognizable postures'; 2) 'registered movements in unambiguous situations i.e. fights, copulations' etc.; 3) they did the 'same in situations where a mixture of drives might be involved'; 4) all situations with a given movement are compared. (Tinbergen, 27th April, 1952, full text is above). Moynihan's observations follow this almost verbatim, and his analysis builds from this directly: he starts with the observable movement (choking); watches it in distinct situations; also in mixed drive conflict situations; finally he compares these situations and similar ones and tries to untangle the strengths of relative drives in these situations, by comparing the relative and approximate measurements of the intensity, 'vigor', of these situations and their effect on the displayed behaviours.

Looking to understand the broader context of Moynihan's work, we must recall that it was a product of the era of the ethogram, and all his observations and their analyses must be seen in relation to it. He was collecting qualitative observations and then analysing them so that he could put together a framework for understanding the whole package of the behaviour of the species he was studying. Moynihan's whole thesis can be seen as one facet of a wider study of the complete behavioural catalogue of the blackheaded gull – a mythical ethogram that was never actually completed. The title sets the smallness of the scale that he felt he was writing on: 'Some Aspects of the Reproductive Behavior of the Black–headed Gull and Related Species'. This suggests why it was that the ideal of the ethogram did not far outlive this very early stage of the Tinbergians, as a practical research agenda it was just too large, and perhaps paradoxically also too small. It was too large, because it represented far too much data to practically write up as either a thesis, book or article; but it was also too small because Tinbergen still viewed it as a necessary precursor to analysis, Desmond Morris, another Tinbergen student for example described it as his 'initial task' (Morris, 2006:74). Furthermore, it is impossible to describe all of the characteristics, movements and behaviours of a species before one

analyses them, as deciding what counts as one or another will always involve a certain amount of experience–led intuitive analysis– e.g. "it's the Oblique rather than the Forward", and one of the natural ways to do this is to look at the context– one comes with fighting the other with mating, or vice versa. Nevertheless Moynihan's work came nearest to the Tinbergian ideal for two reasons – firstly that he attempted to build an ethogram, and secondly that it was built on a very long period of intensive field study, coupled with a smattering of comparative work, in order to see similar behaviours in related species.

Conclusion: *From the field to the Ethogram*

This chapter has looked at the backgrounds and early fieldwork of ethologists in general and specifically focusing on the Tinbergians, particularly lookedat the work of two of Tinbergen's students, Robert Hinde, and Martin Moynihan. This pair were examined as Hinde's work at Oxford began prior to Tinbergen's arrival, whereas Moynihan's was just as Tinbergen was solidly establishing the practices of the school. Hinde's research was subject to a range of influences some of which pre–dated Tinbergen's arrival, and some of which are directly attributable to Tinbergen himself. Moynihan's research fitted with a Tinbergen who was already well ensconced in the Oxford surroundings, and his represents the most faithful attempt to produce what Tinbergen had stated were his ideal research methods. Nevertheless both of Tinbergen's students that I have investigated in this chapter, Hinde and Moynihan, were strongly influenced by him, and shared a great deal in terms of their Tinbergian inheritance.

To suggest that all of the similarities Hinde and Moynihan shared were due to their time with Tinbergen would be untrue, as some came from their parallel life histories prior to their arrival at Oxford, as was common to the general background of most ethologists. However Hinde and Moynihan had further similarities in their life–histories as well, both were recently demobilised from the military, both had been amateur birdwatchers prior to their arrival and both had maintained a childhood interest in animals which they had decided to turn into adult careers. This should

make it unsurprising that their outlooks prior to arriving in Oxford were similar, but in addition to this their relationship with Tinbergen meant that they acquired similarities in their theoretical outlook and methodologies. Once they had worked with Tinbergen, Hinde and Moynihan both made use of Tinbergen's theoretical heritage, which was the subject of the first section in the chapter. Tinbergen's writing on methods influenced both of them, through his insistence on observation on the basis of analysis, and through his interest in comparative studies, and its relationship with notions of attempting comparative morphologies of behaviour.

There were also clear differences between the two students' work, which we can see at least partly as a result of the university context of the research, in which Hinde had been open to other influences from the ornithology department, whereas Moynihan's work had been almost purely Tinbergian.

Hinde's research was eclectic in its methodologies and also in its objects of study. Hinde was comfortable making use of auxiliary recording techniques and technologies, something that was quite different from Tinbergen's approach of direct observation, and from Moynihan who was more faithful in his following of Tinbergen. Hinde had open to him all the resources both practical and intellectual of the ornithology institute to which he was attached (unlike Tinbergen's later students), and with that he chose to make a research project which used amongst its techniques ringing, capture and release, and automatic recording. On Tinbergen's arrival there was an impetus in a new direction, and so some of his analysis had a distinctly Tinbergian flavour, as we saw above. There were sections in his observations and his analysis on certain postures, clearly areas which have a direct relationship with Tinbergen's writing on methods which we saw above, where Tinbergen had described the importance of observing behaviour posture–by–posture. Other research objects of Hinde's however do not show such clear Tinbergian roots, as we saw with the example of the behaviour 'flying off with food', which was a very much more complex category than the postures described by Tinbergen. It was a more complex label because it contained many more assumptions concerning the purpose of the behaviour than would become the norm at the height of the Tinbergians. Following

Tinbergen's own writings his later students bracketed off the possible purposes of the behaviour prior to labelling.

The self–denying ordinance not to involve assumptions of function in labelling of behaviours or movements was a doctrine that Moynihan, a student under Tinbergen's total supervision, adhered to strictly. His work therefore became a patchwork of postures and observations and analyses of small, tightly defined behaviours like choking. Moynihan's research principally consisted of observations of gulls and represents a core contribution to the output of the Tinbergians, and it is easy to discern its influence both in the writings of later Tinbergians and also also in their very similar, and similarly self–denying observations and descriptions, as we will see in chapter four. Indeed the hold of Tinbergen's approach to field observation and analysis, of the work which Hinde had been touched by, but which had become distilled in Moynihan's thesis, would become so powerful that it would dominate the laboratory that Tinbergen was setting up in Oxford in the same period, and which will be introduced to in the next chapter. The Moynihan approach, using minimal intervention, and maximum observation aimed at building Tinbergen's ethograms, and partially theoretically underpinned by the heritage of comparative morphology would characterise the bulk of the early school's fieldwork, but would colour the laboratory as well, in both its practises and also, as we shall see, in its ethos.

There was a strong pattern in the student intake to his school, and also into ethology generally, that early in life these people had felt a dedication to animals and nature – frequently towards birds; an interest that sustained itself in spite of what quite often were laboratory–bound undergraduate biology degrees. For the fieldworkers of the Tinbergians specifically, the early interest was almost always in birds – hardly surprising since Tinbergen had built his reputation on his bird studies primarily, and was also well known for communicating to the amateur ornithological audience, a topic I will pick up in chapter five. I have no doubt that Tinbergen's status as a leading ornithologist helped draw so many ornithologically inclined students to him.

This prior amateur interest was then shaped into learning to observe in the Tinbergian

way, which as we shall explore in the next chapter meant months–long outdoor direct observations of the gulls they were studying.

Chapter Three: The Early Tinbergen Laboratory

Introduction

Tinbergen was a field man to begin with. Almost every public image, photograph or description of him that remains has him, face against the wind and binoculars hung from his neck. Yet much of his time, and that of his students was spent in the laboratory observing animals there or performing experiments on them or with them. Some of the most evocative descriptions that we get of life amongst the Tinbergians come from this laboratory situation, and yet in Hans Kruuk's description it is 'Niko's other world', (2003:235). This is a very good reason to take an interest in the work of the Tinbergians in the laboratory, as it reflects the lack of critical attention that Tinbergen's laboratory has had relative to the more celebrated field studies. Redressing this critical balance is not the only reason to venture into the Tinbergian laboratory, as it was as productive as the field in terms of key published articles, a fact often overlooked because of the way that what was done there was reported. The famous stickleback work, for example, was all done in the laboratory, and though it may have been little commented upon until now, Margaret Bastock's work on Drosophila may also have played a role in bridging the gap between the claims made about the observations of species in the field and the laboratory work of geneticists and synthesisers like Ernst Mayr.

The early Tinbergen laboratory did have key differences from the field, and not just the brute differences of place, but also substantially different practices including quite different relationships between the scientist and their animal research subject. The primacy of place in natural history research has been much discussed, both in the literature, and also in the previous chapters of this thesis, however it will remain a key theme of this section. Work by both Burkhardt (2000) and Kohler (2002a; 2002b; 2002c) on the subject has also demonstrated the value of an approach which investigates the spatial setting of research. Tinbergen's laboratory was set in, around, and on top of the old zoology building in Oxford. Given that what would emerge from this building was some of the most influential research on animal behaviour in

the period, it is worth reproducing Kruuk's description of the rather 'quaint' conditions of the laboratory itself:

> The group atmosphere was helped tremendously by the far from comfortable conditions of the old Zoology Department, next to the University Museum in Parks Road... It was a place with great character, with old bricks and nooks and crannies. There was an us–against–them atmosphere, full of ideas, but with few facilities; everyone was desperately short of space, but never mind, they put up wooden prefab huts on the flat roof, as well as large bird cages in which to keep animals. Niko encouraged the do–it–yourself ideas, which fitted in exactly with his frugality ethos. This went to such lengths that he rather disapproved when Desmond Morris and Philip Guiton started to buy tubifex from an aquarium shop to feed their experimental animals: he expected them to catch earthworms themselves, and chop them up as fish food. (Kruuk, 2003:167).

Hidden in nooks and scattered in rooftop prefab huts, Tinbergen's laboratory was a unique arena, as much an observatory as a conventional laboratory. Within this rather eccentric sounding space, Tinbergen's students were developing new ways to look at and to record the behaviours of their animals.

Section 1: Queer Fish, Vibrating Fruit flies, and Bored Pilchards

The title for this section suggests the challenges for the early Tinbergian laboratory. “Queer fish” was how J.B.S. Haldane described Morris's discovery of homosexuality in sticklebacks, (Morris, 1979:116).[110] Vibrations in Drosophila were a crucial part of of Margaret Bastock's observations, and boredom or just “milling” around were problems for J. Mike Cullen's studies of Pilchard schooling (Cullen, et al. 1965:5). This section will bring out the very different relationship that existed between the laboratory scientists in Tinbergen’s lab and their animals. I will set out how the hard

110Morris lists J.B.S. Haldane as a fan of his homosexuality paper – Haldane congratulated him on it saying he thought it 'not bad for a first paper' (Morris, 2006:111).

space of the laboratory was constructed through observational and social practice and ethos. This relationship was based on a different observer style to the one we have seen in the previous chapter, as it involves considerably more solid and reproducible ways of observing. There are three principal sources of evidence that we have for this. The first is from Desmond Morris's autobiographies, in which the same stories recur across his several editions. The second is Margaret Bastock's work on that titan of biological research, the Drosophila. The third is in the work of J. Mike Cullen, a key figure in the Tinbergians, who is also an unusual figure in being a creature of both the field and the lab, to an extent unusual for their school.

Section 1.1 Desmond Morris, Sticklebacks and Ethograms

Desmond Morris's ever colourful and entertaining autobiographies give a real sense of his time in the Tinbergians in Oxford. Amidst the lighter anecdotes, the ribaldry and the indiscreet revelations about fellow ethologists Morris does slip in a passage on the drudgery of everyday experimentation in the Tinbergen laboratory. Though I have touched on it elsewhere, there really is no other source which gives quite as rich an account of the way of life in Tinbergen's laboratory and so I shall return to it here. Morris concisely describes his observational set up:

> The animal I chose from the list of five was the ten–spined Stickleback. I had already kept the more common, three spined species and had briefly studied its extraordinarily complex breeding cycle, so that I felt I had a head start with sticklebacks. I would find the practical problems of setting up research aquaria comparatively easy and, furthermore, I happened to know an excellent ten–spined stickleback river – Marlborough, only an hour's drive away. So collecting them would be no problem.
>
> There was the added advantage that Niko himself had already made extensive studies of three–spined fish,[111] which would enable me to carry

111 In her wry "stickleback's–eye–view" of the history of the journal *Animal Behaviour*, Huntingford notes the centrality of stickleback work to the Tinbergians, but also elaborates the type of work that they were known for at that time:

> 'Thanks to Niko Tinbergen, sticklebacks have been famous since the beginning of ethological time for their nuptial coloration and its role as an aggression–eliciting stimulus and for their zig–zag courtship behaviour.' (Huntingford, 2003:2)
>
> The type of stickleback work here described is exactly that which Desmond Morris was involved with, stimulus and response, and extremely close observation

> out a comparative investigation – seeing how and why the two species differed.[112] It was agreed that I should become a sticklebacker.
>
> I was allocated a basement room because it was suitably cool for the fish, which I shared with Philip Guiton, another new student of Niko's, who was also going to be doing his D.Phil. studies on sticklebacks. Together we set up row upon row of aquarium tanks until there was hardly room left for us to move about. Surrounded by about fifty of these tanks we had to slide our way around between them, planting water–weeds, fitting aerators, and adjusting lighting covers. Then we set out in the departmental Land Rover on collecting trips, stocking our fish room until it was almost as if we were living submerged in a densely populated river. With fishwatching, it was difficult to take the laboratory into the field, so instead we brought the field into the laboratory. (Morris, 1979:74)

This idea of bringing the field into the laboratory was crucial for the Tinbergians whose principal object of study was the natural behaviour of species, even in a laboratory environment. Morris even describes Tinbergen's disapproval of his buying rather than digging up worms to feed the experimental subjects. On a research level there is no difference that anyone mentions between wild collected and commercially supplied worms, but as this was something that was very far from Tinbergen's idea of fieldwork it was not looked on fondly – 'for Niko it lacked the dignity of labour.' (Morris, 1979:75). Kruuk suggests that what offended Tinbergen most about this is that it went against his 'frugality ethos', (Kruuk, 2003:167), which had its roots both in his lengthy times in the fields, and perhaps also the impact of his harrowing wartime experiences. Morris, a very different figure to Tinbergen, was much more urbane also having interests in painting, film–making, and applying his mind directly to humans in The Naked Ape (1968).[113] Even more significantly Morris was

---

under what were attempted to be as natural a set of conditions as could be created in a laboratory setting.

112 There is a direct field–laboratory comparison at this point, in that Moynihan took the blackheaded gull as a related case to the herring gull, which Tinbergen had already done intense field study on, and here Morris studied a stickleback that was closely related to one that Tinbergen had also previously studied. The school then was building comparisons and looking for behavioural homologies in the laboratory, in a similar manner to the way that they were working in the field.

113 Tinbergen's life was very austere, something that made him ill–fitted for the life of an Oxford don, Kruuk argues that he was ill–suited to the Oxford life, as he disliked pomp, college life and all the

definitely not a fieldworker, and had little interest in the kinds of 'character forming' experiences that were the basis of cold and uncomfortable fieldwork. As a laboratory worker, however, Morris did contribute enormously to the school's output, and later as a public intellectual, to its prestige in the British public realm. Morris's work was built on relatively simple observation techniques combined with his own methods of recording behaviour, using a typewriter rather than a pen and notebook. His autobiographical writing points to how his research fitted into the standard practices of the laboratory, in which first there is literature learning, and then observation of the full annual life–cycle of the stickleback:

> During my first winter in Oxford I read up all the existing literature on the stickleback and in the laboratory examined its winter shoaling behaviour. Then in the following spring, came my first major research phases, as the breeding season approached. My main task was to analyse the reproductive cycle of the species and this was condensed into a period of a few months, starting in late February and extending through March, April and May, and petering out in June. It was a time of frenzied activity for the sticklebacks in my tanks and a time of endless hours of crouched watching for me. My facility for fast typing was a godsend, as I could sit in front of my tanks thumping out a running commentary of the behaviour sequences as they were actually occurring. (Morris, 1979:78–9

Morris then describes the way that he sought to construct an *ethogram*, which bears out the differences between what is possible to a laboratory observer and what is not possible for their fieldworking counterparts. All of the behaviours were available to be observed and analysed, in a way impossible in the field, because Morris had to sit and record everything on his typewriter, and because the tank was the only space possible to observe – there is no 'just–flying–away' for a stickleback – there was the possibility of total recording, something suggested by the fact that Morris isolated 45 stickleback actions (Morris, 1979:77), something in strong contrast to, for example,

trimmings of high table (Kruuk, 2003:193–4). Morris, by contrast, was brash and fascinated by a large range of areas outside of his science, including art, and conversation, and held exhibitions of his paintings, as well as producing scientific papers in his time at Oxford.

Martin Moynihan, whose analysis we examined in the last chapter, and who focused on only a handful of behaviours and postures. Morris first described how important it was to build an ethogram, even though he was based in the laboratory and was observing under non–natural conditions:

> My initial task – and one that Tinbergen always insisted on – was the compilation of an 'ethogram': that is, a comprehensive list of every action my fish were capable of performing; in other words a complete behaviour repertoire. It was part of the Tinbergen creed that no one should attempt to analyse any one aspect of an animal's behaviour until he had first spent a whole year familiarizing himself with its complete range of activities and had described each in detail. Although for some this seemed like a slow beginning to a research project, Niko claimed that, without it, it was impossible to understand the true lifestyle of the animal. (Morris, 2007:74)

The value of Morris's account is that we can see how his task was set out for him. To be a student in Tinbergen's laboratory was to intensively study behaviour, but it was to do it in a unique way, where the aim was to study the whole behaviour repertoire rather than any one aspect, and to try and record all of the behaviours prior to focussing on any one of them as a suitable case for further study. Morris's work reached closest to Tinbergen's ideal, in that not only did Morris seek to observe and describe all of the behaviours of a species through a whole year, but he tried to do it at a movement–by–movement level:

> In one ninety minute observation, for instance, when I introduced several females into a male's tank, he performed no fewer than 1,925 actions. This required something more than fast typing – it demanded a special code of shorthand. I had isolated forty–five stickleback actions and gave one a symbol of one or two letters. This code then streamed out across the page: PF3 GclockP ZZ B ZZZZZ BB ZZZZ SHW SHV BBBB PF2… and so on, leaving me with countless hours of decoding later in the day.

> But from all of this I was beginning to assemble a picture of what it was like to be a sexy stickleback in the spring. (Morris, 2007:75)

Morris's description makes use of the word “action” in two distinct ways, firstly as a category of movements performed, and secondly as any specific instance of that movement. For example the movement he labelled “Z” represents the first use of action, as a category. Each time it appears on the page it records a specific instance of that action.. The combination of these labelled movements if repeated again and again which were seen as fixed action patterns (FAPs), in order that they could be pronounced 'behaviours' worthy of inclusion in the ethogram list. In spite of the obvious differences between sitting in a laboratory observing movements of fish in tanks and recording them by typing – and being flung out to distant cliffs in order to observe fleeting birds' movements though binoculars, nevertheless Morris seems to have absorbed the field ethos of the school. It is not coincidental that he still chooses to emphasise the discomfort and the seasonality of his work, things that were in common with the fieldworkers of the school. Both sets were involved in 'crouched watching', and also both were tied to the March, April, May, June seasonality of breeding in Britain, even though Morris's sticklebacks were all laboratory–bound.

Desmond Morris's observation diagrams are an object lesson in the demonstration of behaviour. In his well received 'Homosexuality in the Ten–Spined Stickleback' (1951), Morris made use of the kind of behaviour diagrams that would be familiar to anyone who has read Tinbergen's *The Study of Instinct* (published in that year, though written some years earlier), with images of dancing fish, in relatively empty but naturalistic surroundings, and with a surprising amount of detail. Three examples are given below in image 3.1:

[Image 6] (Morris, 1951: 238)

In these diagrams, the key Tinbergian principles are followed, and they can be seen as akin to Moynihan's bird behaviour diagrams of the previous chapter, with a similar naturalistic outlook. Key similarities emerge from each of the diagrams given: the first diagram (Fig. 5 [image 6]) of the dancing male emphasises those morphological

features which are significant for stimulating female sexual responses – the ventral fins – in a manner akin to the famous red–spot diagrams of the herring gulls, seen in the introduction to this thesis, where the focus is on one feature to demonstrate its stimulating function. The second diagram in (Fig. 6 [image 6]) brings to life the stimulus, showing how it is displayed to the female in the pre–copulation dance. The dance itself is illustrated by the dotted line, an arrow, and a fair amount of imagination on the part of the reader. The final image is the male showing the female the entrance to its nest. Although the arrangement of the images makes it somewhat less easy to follow the 'story' directly, the key stages in the early part of the mating sequence are quite clear. More than that though, there is a feeling which overlaps conveyed by these images– Moynihan's exquisite line drawings of courting birds here have a less skilled but still empathetic correlate. Indeed Moynihan's images, which typically showed the birds themselves and a hint of grass, or a flash of the nests but very little more to confuse the eye, really does have a counterpart in (Fig.7

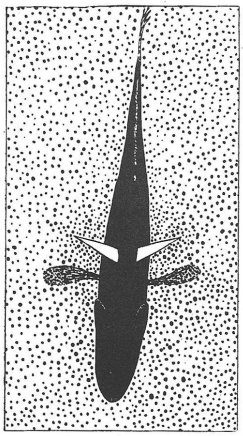


Fig. 5.

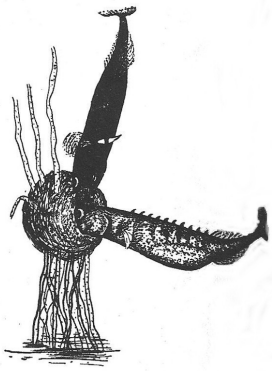


Fig. 7.

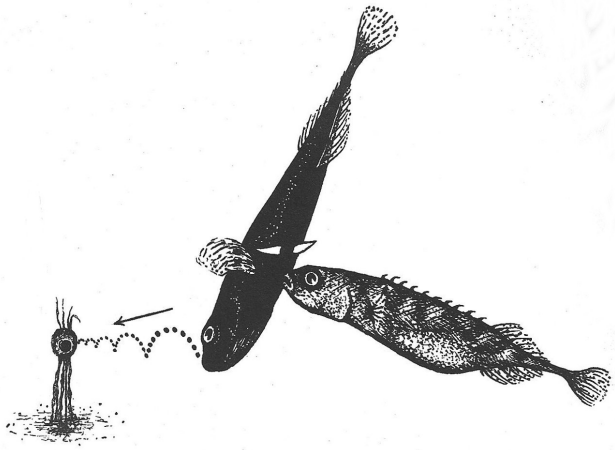


Fig. 6.

Fig. 5. The ventral surface of the dancing male as seen by the female, showing the conspicuous white spines against the black body.
Fig. 6. Courtship C. Nest-oriented dancing. The male swims to the nest in short inclined jumps, followed closely by the female.
Fig. 7. Courtship D. The male shows the nest-entrance to the female by fanning in the tilted position. The female pushes into the entrance with her nose.

[image 6]) which has exactly that, the two animals, their nest and a little grass in which it is embedded.

The second type of images in Morris's work take a geographical approach to demonstrating behaviour. The diagram below locates the territories of male sticklebacks, shown from above, and without any actual diagrammatic representation of the fish themselves. Instead there is a highly abstracted view, in which letters replace fish, and dots and lines show the main features of the large fish–tank.

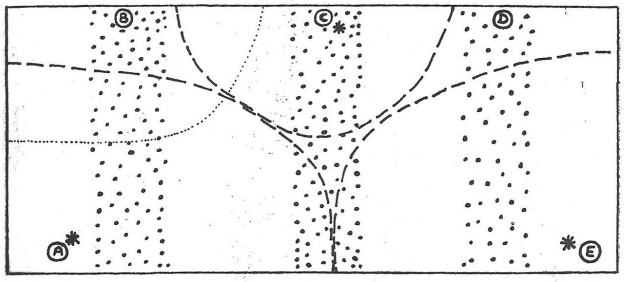


Fig. 2. Tank Plan showing territory areas at a particular stage of the experiment. The dotted areas are the three hedgerows of Willowmoss. The 5 points A B C D & E are the positions of the five clumps of Myriophyllum. The broken lines represent the territory boundaries, and the asterisks show the positions of the three nests present at the time. There were five male fish in the tank, and one of the nestless males spent much of its time at B. It was unable to build, as it was repeatedly molested by the male at A, but when the latter's nest was damaged and abandoned, the fish at B quickly built and formed the territory shown by the fine dotted line. Later a similar change-over occurred between fish at D & E.

[Image 7] (Morris, 1951:235)

This image is vastly different to those of the behavioural type which have been discussed before. It shows the kind of abstracted data that you might more expect of an ecologist, studying the interaction between animal and environment, rather than the behaviourally focused Tinbergians. However this is as based upon the *same kind of Tinbergian observation* that characterised the behavioural diagrams because fish territories can only be identified by prolonged observation. This is because there are no fixed markers that can be identified – unlike a dog's territory,where it would be possible to test the trees for scent marking and thus easily draw boundaries – with fish territory can only be identified by observing behaviours. One must observe closely to see at what points certain aggressive behaviours are seen by a fish, and at what point defensive behaviours, and from there infer from these behavioural reactions where the boundaries between territories may lie. *Morris's diagram is an attempt to create a two dimensional record of a four dimensional phenomenon – the territories of sticklebacks as defined by their behaviours.* Even the brief label below the diagram is a social life in miniature, with a description of the conditions in the tank followed by explanations of the changing social territories of the fish therein. This second type of image although quite different in appearance and in informational content, remains built on the same observations that underlay the more familiar behavioural images of the Tinbergians, as is affirmed by Morris in the continuing text below the diagram:

> As was expected, a great deal of fighting and threatening was seen as a result of this crowding, but another particularly interesting behaviour pattern was also accidentally brought to light, apparently as a result of this particular population density. This was the phenomenon of homosexuality on the part of certain males. This homosexual behaviour took the form both of lack of discrimination where a sexual partner was concerned (on the part of dominant males), and of the inversion of the complete sexual pattern (on the part of the dominated males). (Morris, 1951:235)

Morris' waspish suggestion that there was a 'lack of discrimination where a sexual partner was concerned', might have implied that there was confusion or mis–stimulation amongst his fish, but his overall message is quite clear. One important consequence of 'crowding' is behavioural rather than for example nutritional, morphological or similar – essentially it is about *what they do* rather than *what happens to them*, as would be the case of a purely ecological study. That is seeing the fish with the Tinbergian eye.

How starkly different Morris's stickleback is to that of his contemporaries is illustrated by comparison with them. For example, working at the same time in Britain, H.B.N. Hynes at Liverpool University worked on a variety of questions about sticklebacks. He worked on their food consumption, and had an interest in their life history, which led to looking at ecological questions. How distant they were from the type of work that Morris was doing can be seen in the methods section of the paper by Hynes (with Jones, 1950) in which the principal object of study was the life–history of the stickleback, but where the only data they considered significant were age rings on stickleback otoliths.[114] Hynes and Jones described how they

114An otolith taking the **O.E.D.** Definition is: Any of the calcareous particles found in the inner ear of vertebrates or the otocyst of invertebrates, which are involved in the perception of gravitational forces (and, in fishes, of sound) and the maintenance of balance and orientation; (also) a collection of such particles in the gelatinous membrane overlying the macula of the utricle or saccule. Also called *statolith*.
In many fishes the otolith is a large, well–developed body with a characteristic shape and a pattern of growth rings by which the fish can be aged.

captured wild sticklebacks in the field and preserved them in alcohol (Hynes & Jones, 1950:62). They then sought to find a way of ageing the fish, something they discovered could best be done by looking at annual rings on the otolith, in order that they could understand the age structures of the wild populations of stickleback as a way to comprehend what they saw as the life–history of the stickleback (Ibid).

I specifically chose Hynes' work because Morris evidently read Hynes (1950) work, as he referenced it directly in the homosexuality paper of 1951 (Morris, 1951: 260). I have not traced a link with this particular paper just mentioned (Hynes and Jones, 1950), which on first sight might seem surprising as Hynes takes a more ecological approach here than he did in the 1950 paper referenced by Morris. Hynes's papers, even at their most ecological are written in a very different scientific mode to Morris's with vastly different methods and underlying philosophies. Hynes treated the field as a place for collecting samples, with the main body of the research being performed in the laboratory on the preserved specimens. When Hynes did return to the laboratory it was in the company of dead specimens for examination, rather than with live animals to study their behavioural interactions with their environment. The key stages in Hynes's methodology are: firstly preservation in alcohol; secondly measurement of the specimens particularly from fin to tail and from snout to tail and this was recorded; thirdly they extracted the otolith (a bony inner ear fragment) for further examination. Annulations on the otioliths provided a basic way to age the fish (though obviously not one it is possible to perform whilst the fish is itself still alive), from which Hynes was able to build a life–history of the sticklebacks that he had studied, using the ages at which they reached maturity, mated and died.

Hynes's work produced a radically different type of 'life–history' to that produced by the Tinbergians. The reason that Hynes's work and Morris's form such a stark contrast is not just a difference in interests, but a difference in scientific outlook, in which Morris was interested principally in live animals and recording their lives in an ethogram, whereas Hynes saw dissection as the route to understanding them. Morris's approach also differed from the Behaviorists, however, even though they took live animals into the laboratory, as they were uninterested in natural or innate

behaviours. These comparisons reveal two prior decisions that Morris made, firstly to observe rather than dissect (as Hynes had done), and secondly to observe rather than experiment upon (unlike the Behaviorists). Both of these decisions locate Morris as a classic laboratory Tinbergian, interested in the same questions, and making use of the same methods and ethos as his fieldworking colleagues.

Section 1.2 Margaret Bastock's Drosophila linking behaviour and genetics

Looking beyond the ethos and into the theoretical content of the school, there were further strong links between the field and the laboratory in the shape of the Drosophila work of Margaret Bastock. Bastock's work, which Tinbergen's mentioned frequently to Ernst Mayr,[115] provided a direct link between the kind of laboratory studies that geneticists of the Modern Synthesis generation had done and the behavioural work of the Tinbergians. Mayr's role, both in the Modern Synthesis and his interest in bird behaviour, was paralleled in Britain by Julian Huxley, but these studies, on the one hand of population genetics and on the other of behaviour, rarely overlapped, even though both sides were interested. Mayr, for example, used his studies of wild Papuan kingfishers (*Tanysiptera hydrocharis–galatea*)[116] as the basis of much of his genetic theorising rather than primarily for behavioural work, whereas Tinbergen and his students in the early period were far more concerned with behaviour and touched evolution in the adaptive sense rather than through a

115Bastock and related Drosophila work is mentioned frequently in the correspondence between Mayr and Tinbergen in the early 1950s, for example see Mayr to Tinbergen, September 28, 1950, or Tinbergen to Mayr, Oct. 5, 1950, (HUG(FP) 14.7 Box 8 folder 372). There are many other letters in the period during which Bastock was resident, and even some after she had moved to Edinburgh, following her marriage to Aubrey Manning.

116Kohler, in *All Creatures* (2006), which is about Collectors in late Nineteenth Century and Early Twentieth Century Natural History, indicates that Mayr's use of trinomials like this is one of the very last taxonomic uses, before subspecies names (the last word of the three) were dropped in the discipline. In one of the most interesting discussions of the book he describes the switch from Linnean binomials to subspecies trinomials in the nineteenth century, and the switch back to binomials in the twentieth, and in which Mayr was on the 'losing' side of the debate, being strongly in favour of the retention of trinomials, characteristic of museum taxonomists and in contrast to the young Turks of the discipline, such as E.O. Wilson who saw trinomials as 'arbitrary and authoritarian' (Kohler, 2006:265), and who were more inclined to think of populations than species, partly as a consequence of the type of work that Mayr had himself been a part of in the Modern Synthesis.

consideration of genetics. Here is a characteristic passage from Mayr, in Huxley, Hardy & Ford's Evolution as a Process (1954), to which Tinbergen also contributed a chapter:

> The evolutionist takes, on the whole, a dim view of the future prospects of populations with depleted genetic variability. Such populations are not very plastic. If they live on an island (in the broad sense of the word), they will probably be successful as long as conditions remain stationary. However, such populations rarely have the capacity to adapt themselves to environmental shocks. The arrival of a new competitor or of a new enemy or a drastic change of vegetation or of the physical environment is apt to lead to extinction. It is no coincidence that even though less than 20 per cent of all species of birds are island birds, more than 90 per cent of all bird species that have become extinct in historical times are island species. An island bird thus has at least fifty times as great a chance to become extinct as a mainland bird. Only part of this extinction can be attributed to the small size of the range of these island species. (Mayr, 1954:173).

The contrast with Tinbergen's piece in the same volume is illustrative, as it too engages with birds, and with evolutionary selection, but brings to it adaptationist approach. This approach focuses on the origins and evolution of a behaviour within a particular species, and its relationship with adaptation and selection. Interestingly Mayr and Tinbergen's pieces can very much be read side–by–side, as was clearly the intention of the authors by including them in the same volume, but though they touch on similar phenomena in birds, namely selection and evolution, they have almost no overlap, either in content or method. Mayr's piece was a statistical consideration of the nature of speciation, in which the object of study was genetic frequencies in populations; Tinbergen's object of study was an observable behaviour, and his interaction with evolutionary concepts went only so far as he could use them to consider the origins and development of that behaviour. Here is Tinbergen's section at its most evolutionary:

> Comparisons of this type enable us to describe the kind of changes which must have occurred when a derived movement,[117] by adaptive evolution, has developed into a highly specialized releaser. In other words, it enables us to describe the course of ritualization. In this process, several principles can be detected which obviously have operated repeatedly. Before enumerating these principles I should stress the fragmentary nature of the evidence. Much more detailed work will have to be done to strengthen the as yet tentative generalizations. Such work must involve detailed description of the movements, analysis of their function, analysis of their origin, and comparison of homologous sets of derived movements together with their originals in a number of closely related species. I should add that it is only possible to establish homologies if the causation is understood as well. (Tinbergen, 1954:241)

The distance between the approaches that these two extracts show is considerable, and it is this distance combined with prodding from Mayr which spurred Tinbergen to develop a Drosophila programme.[118] But the Tinbergians' Drosophila work was profoundly different to the type of population genetics that had previously made such frequent use of Drosophila, bringing a behavioural and adaptationist focus. Margaret Bastock's work sits as a link between the behavioural and genetic aspects of biology, and in a manner that we should now see as an echo of Tinbergian field research. Bastock, before outlining her genetic study of differential breeding patterns in yellow and wild stocks of *Drosophila melanogaster*, gives a very brief description of their behaviour patterns. Indeed she begins by suggesting that no description is needed, because it has been covered by so many other people (Bastock, 1956:423), and yet still gives a lengthy account. Here, for example is a short extract:

117 The idea of 'derived activities' was how Tinbergen categorised complex movements which had evolved from previous behaviours in predecessor species. These derived activities evolved into contextually out–of–place behaviours, which did not fit into the patterns he had elsewhere described, or fitted only parts of the patterns. He argued that they were derived from earlier behaviour patterns, and called the out of place movements 'displacement activities' and the partial movements 'intention activities' (Tinbergen, 1952:30).

118 Tinbergen's letters show that Mayr had suggested beginning studies on Drosophila by March of 1948, the year before he arrived in Oxford. See Tinbergen to Mayr, 28th March, 1948. HUG(FP) 14.7 Box 4 folder 197

> At the beginning of courtship the male stands facing the female, usually in the position from which he has approached, whether it be at the side of, in front of, or behind her. (Spieth[119] says that he always circles to the rear immediately but I do not agree with this, and Sturtevant[120] also observed that he would stand in any position relative to the female.) If the female moves off, the male will follow, and this of course brings him behind her, but often the female stands still and then he does not at first change his position. I have called this part of the courtship *orientation*, irrespective of whether the male is following or standing. (Bastock: 1956:423).

The use of the term 'orientation' here is absolutely central, this is where Bastock shows that she is still, in a profound sense, a Tinbergian. This is because there is a significant overlap in the approach to understanding and recording behaviour between her work and that of her fieldworking colleagues. Her use of the term *orientation* is analogous to the terms that the fieldworkers used, for example where they recorded 'Oblique' or 'Upright' postures, in that they serve the same purpose, albeit in a very different physical and scientific space. 'Orientation' is a unit of behaviour, of equal significance to 'vibrating' behaviour that she identified, and just as much a unit as the oblique posture – though interestingly one that could be either standing still, or if they were not facing in the standard direction, movement until they were. At the same time it maintains a kinship with the approach described by Desmond Morris above, with his frenetic typing out of all of the individual actions of his sticklebacks, which he used as the basis for his analysis of their behaviour patterns. Bastock's next step is to show the recordings of various wild Drosophila's

119Herman Spieth was an American Drosophila researcher at the University of California, who was known to the Tinbergians for his work focused on the behaviour of Drosophila, which he published in *Behaviour*, a journal that Tinbergen himself had helped to set up, and at this point remained upon the editorial board. Spieth's paper on the mating behaviour of Drosophila was a considerable work at over 40 pages in length, and working in great detail. Naturally this approach recommended itself to the Tinbergians, even though the Drosophila itself was something of a standard bearer for classical genetics rather than behaviour work. See Spieth (1951:105–145).

120Alfred Sturtevant was a T.H. Morgan–trained Drosophila geneticist, who by this period was the Professor of Genetics at the California Institute of Technology. In his early years he maintained an interest in both genetical studies of Drosophila and taxonomical studies, producing a lengthy work on North American Drosophila species (Sturtevant, 1952). He has a full National Academy of Sciences Biographical Memoir, (Lewis, E.B., 1976).

mating patterns:

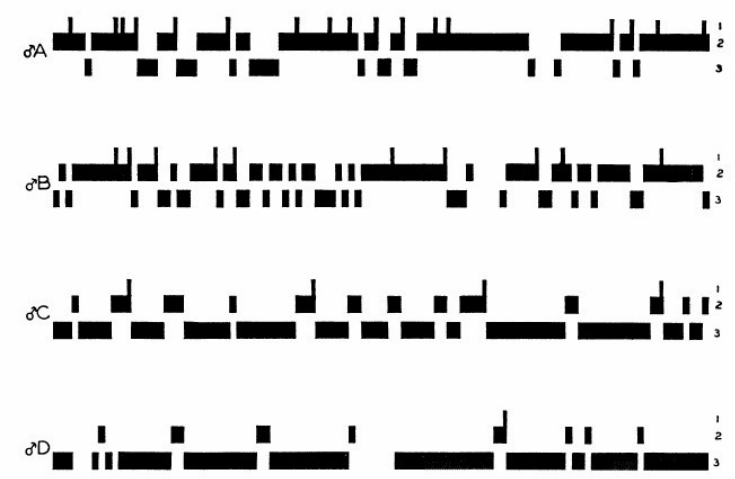


FIG. 2. Diagrammatic representation of the courtship patterns of four wild *D. melanogaster* males, each with a virgin wild type female. 1. licking; 2. vibration; 3. orientation.

[Image 9] (Bastock, 1956: 424)

These are records of male Drosophila mating patterns, detailing 'licking', 'vibrating' and 'orientation' behavioural patterns. The diagram is simple, if not intuitive to read. Each of the four main left–right lines represents one Drosophila male's behaviour during courtship. It is split into three, which represent three different behaviours. The top space is time spent licking, the second or middle space is time spent vibrating, and the bottom or third space is time spent performing orientation behaviour. These observations formed the basis for her comparative studies of two different groups of Drosophila, one a wild population, and one a mutant population of yellow Drosophila. What she showed was that there was a significant difference in mating behaviour between the two populations, and this led to differences in the mating success. Furthermore she demonstrated that this was due to differences in the behaviour between the two Drosophila populations rather than differences in how stimulating their colours were.[121] Specifically she showed that yellow Drosophila spent less time on the highly stimulating *vibrating* behaviour and replaced it with less stimulating *orientation* behaviour (Bastock, 1956: 437). The yellow Drosophila were chosen only because they were a separate population with different behavioural characteristics not because of differences in their colour. She was choosing the

121Bastock built on Spieth's work which had showed that colour differentiation was not a factor in stimulation in Drosophila. (Spieth, 1951)

opposite case to her birdwatching colleagues, a species where colour differentiation made no difference to stimulation patterns, but behaviour patterns did. She saw that yellow Drosophila were 'more lethargic in their courtship' (Bastock, 1956:433) but by observing their mating in the dark she could show that their colour was not the determining stimulation factor. Behavioural differences that happened to be correlated with colour were what caused the mating success. The difference was stark, and remained so even when the Drosophila were allowed to mate in the light (though unsurprisingly their overall success rate improved considerably), as she showed in the pair of graphs below.

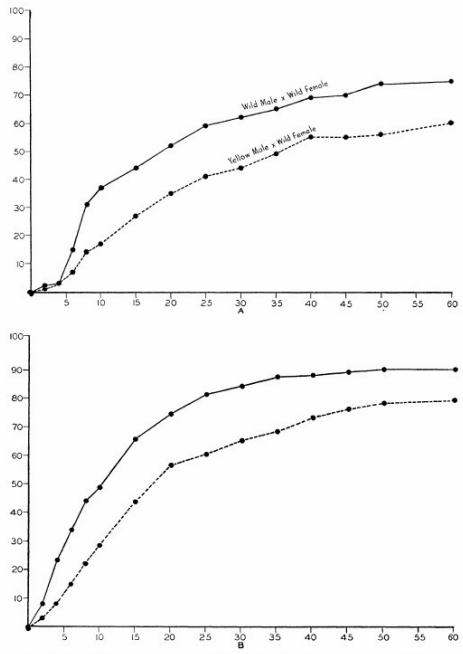


FIG. 5. A. Mating success compared for wild and yellow males with wild females in DARK in pair matings. Average time from introduction to copulation in DARK: wild male × wild female: 16.0 minutes; yellow male × wild female: 20.9 minutes. B. Controls tested simultaneously in the LIGHT. Average time from introduction to copulation in LIGHT: wild male × wild female: 11.4 minutes; yellow male × wild female: 17.6 minutes. The wild and yellow stocks had been previously intercrossed for 7 generations. Abscissa: time in minutes from introduction. Ordinate: % of successful males. Dashed line: yellow male × wild female. Solid line: wild male × wild female.

[Image 10] (Bastock, 1956:432)

The two graphs shown above demonstrate quite why it was that Bastock was so excited by her observations. At the top is a graph showing mating success (i.e. completed copulations) against time in minutes for both wild type and laboratory–bred yellow Drosophila observed in darkness. Below it is a graph showing the control experiment in which the two types were observed in the light. There are distinctions between and within the graphs which are immediately apparent. Firstly contrasting the two graphs it is clear that overall mating success rate is higher in the light than in the darkness, but far more significantly, that under both conditions there

were observable differences between the wild Drosophila group and the laboratory–bred yellow strain. She understood the significance of her own research:

> My conclusion, therefore, although speculative, is that this gene mutation in Drosophila melanogaster does change the pattern of courtship behavior in a manner which may well have been used in evolution. Such an effect of a single gene mutation upon the frequency of elements in a behavior pattern has, I think, not previously been demonstrated. (Bastock, 1956: 437–438)

Tinbergen's interest in evolutionary questions could then be justified: behaviour could be both a factor affected by evolution, and a motor for it – though Bastock had not specified a mechanism for this. This might have given his own and his group's fieldwork far wider significance than they had previously been able to claim. It is one thing to claim that there are certain observable stimuli for animal behaviour, quite another to suggest that studies of behaviour could contribute to evolutionary debates. However Tinbergen chose not to publicly give great weight to Bastock's work, indeed it is hard to see where he mentions it outside of his correspondence with Mayr. Perhaps then Bastock's work represents a missed opportunity, as from this point on Tinbergen could have chosen to treat Evolution as a subject that was wholly his own, and not merely the preserve of geneticists, morphologists and taxonomists, because here was evidence that behaviour was influenced by genes, and therefore by heredity and evolution of the modern synthesis type.[122]

122 Writing about Tinbergen's later student Richard Dawkins, Marek Kohn repeats the observation that evolution and genetics had already come together in the Tinbergians by the time (in 1960) that Dawkins had arrived. Interestingly Kohn makes only one mention of Bastock, and this is in relation to John Maynard Smith's debate with Helen Spurway over Drosophila behaviour, rather than in relation to Bastock's own work. Kohn describes how the two aspects genetics and behaviour had come together:

> In 1963, the year after Dawkins graduated, Tinbergen set out the terms of ethological enquiry into animal behaviour. Ethologists could ask how a behaviour evolved within a lineage and how it developed within an individual animal. They could ask about its proximate causes, the events within the body and outside it that were involved in its occurrence, and they could also ask about its ultimate causes, its function and its survival value. Dawkins identified himself as a functional ethologist, meaning that he was concerned with ultimate adaptive causes. By the time he reached Oxford, he [Dawkins] considers, they had also become Tinbergen's principal concern. Oxford's field genetics and field behavioural studies converged on the theme of selection. (Kohn, 2004:308)

Understanding the difficult place that Bastock fits in the Tinbergian milieu is crucial but challenging. Burkhardt gave her little more than a walk–on part,[123] as did Kohn (see footnote above), and Kruuk, and it seems Tinbergen himself, was not clear about the importance of her work. Tinbergen suggested that he only 'tolerated it, welcomed it, but could not understand it' (Tinbergen in Kruuk, 2003:166),[124] which is hardly a ringing endorsement, and certainly suggests that he saw it as peripheral to his overall work. The only historical consideration of Bastock's contribution comes from Cobb (2007), who, wrote as a biologist on the lessons her work might give for an audience of contemporary biologists.[125] This demonstrates the lack of attention this work has had by historians, and by Tinbergen's own writing after she had left Oxford in the 1960s. However both Kruuk and Burkhardt argue that Tinbergen was proud of the work of Margaret Bastock's student Stella Crossley on the same subject and both Kruuk and Burkhardt attributed the discovery that change in behaviour could be caused by genetics to Crossley. 'It was a result Niko was proud of, despite his lack of interest in genetics, because it suggested how natural selection pressures could affect behaviour.' (Kruuk, 2003:186) However the detail of the study certainly shows that Crossley's work was merely a follow-on study from Bastock's, and that what was seen as a result to be proud of was a subsidiary result to that already achieved by Bastock.[126]

That Bastock's work was recalled only in relation to her own student's work is perhaps unfortunate from a historiographical perspective, but probably representative of the way that the school sidelined her work in their memories. Kruuk was very

123 Bastock gets only two mentions for her work in Burkhardt (2005), the first of which was for a graduate paper with Morris on derived activities and the second for a pointer to her influence on Stella Crossley who worked on Drosophila under her supervision. Morris himself leaves her out of his autobiographical writings, which given that they shared a laboratory, is particularly surprising.

124 This is taken from a letter in the private Manning archive, to which Kruuk was privy, but to which I could not get access. There is no further context in the original quotation, so we must assume that it is being used as intended.

125 Cobb (2007) suggests that Tinbergen was uninterested in genetic studies, skimming past them in his seminal (1963) Aims & Methods paper, and this may have been because Tinbergen may have struggled with some of the mathematical detail of the subject.

126 The result that Kruuk reports Tinbergen as being so proud of is Crossley's: 'She applied artificial 'selection pressures' on one single behaviour pattern in fruit flies, and showed that one could dramatically change the inherited behaviour of a species within forty generations.' (Kruuk, 2003:186) Which is indubitably a subsidiary result to Bastock's work introduced above.

much an insider to the group, and so has passed on at least some of the later feeling of the time, that Crossley's work was the significant bridge between ethology and behavioural genetics, and Burkhardt has taken this trend too. Burkhadt's mention of Bastock is viewed through the lens of Tinbergen and Mayr's correspondence, which contains suggestions that ethology should be moving toward behavioural ecology, with genetics being seen as a peripheral concern. (Burkhardt, 2005:439). Although the Tinbergians clearly believed prior to Bastock's work that behavioural processes were influenced by evolution,[127] Bastock could have given them a much more solid frame for that assertion. Furthermore as it was in part a behaviour study based on direct behavioural observations rather than experiments, it was performed in a kindred language to that of the field research. If we look back into the time when Bastock was doing the research we can see that Tinbergen took quite a different opinion to that expressed later, as he was evidently delighted with Bastock's observations, and he excitedly wrote to Ernst Mayr to inform him of them:

> ... I am also very anxious to hear what you have to say about some of the things we have been doing. The Drosophila work of Miss Bastock has, I think, progressed very well, and she is soon sending a paper on her main results for Evolution; her main result is that there are real differences between wild type and yellow males melanogaster, which she thinks she can reduce to one difference of degree: a shift in the relative strength of the factor underlying sexual motivation, which affects three elements of the sexual behaviour chain that each have a different threshold for the common motivational factor. Further, the work of Esther Cullen on the Kittiwake shows in fascinating detail how many aspects of its behaviour in which it differs from other gulls must be considered the outcome of adaptive radiation connected with the cliff–breeding which is no doubt an anti–predator device. (Tinbergen to Mayr, March 4th 1956)[128]

One of the most striking things about this passage is the linkage that Tinbergen

127For example in the Study of Instinct Tinbergen considers whether behaviour can be seen as adaptive: 'Is all behaviour adaptive, does every instinct contribute to self–maintenance?' (Tinbergen, 1951:152)

128This is from the Mayr correspondence at Harvard, papers HUG(FP) 74.7 Box 4 folder 637.

himself draws between the Bastock's laboratory–based Drosophila work and the work by Esther Cullen on kittiwakes (discussed below), which was based on field observations. To me this could be indicative of the importance he felt Bastock's work had at the time. There must be caution in this conclusion, as Tinbergen was presenting the work of his group to his friend and powerful scientific ally Ernst Mayr, who had been interested in evolution and genetics, and so would have chosen those aspects most interesting to Mayr.

Section 1.3 Mike Cullen bringing pilchards to the laboratory

One person who transcended the field/laboratory line was J. Michael (Mike) Cullen, working as comfortably in the laboratory as in the field, and later being known as a teacher more than an industrious academic publisher.[129] His D.Phil. fieldwork was entirely orthodox, following the established Tinbergian patterns that I described in the previous chapter. It was concerned with the behaviour of the arctic tern, especially courtship, pair–formation, breeding, and the behaviour of the young (J.M. Cullen, 1956:i). This might make his laboratory work seem even more exceptional, as it focussed on a species that was not a Tinbergian staple, the pilchard. Unlike the ten–spined sticklebacks which Morris had studied, pilchards are not closely related to three–spined sticklebacks which Tinbergen had previously studied.

It is characteristic of Mike Cullen's work that his was quite different, and yet retained a kinship with the larger Tinbergian approach. His fieldwork, for example, was on Arctic terns, which again are considerably less closely related to herring gulls than

129In his obituary in *Ibis*, written by John Krebs and Richard Dawkins, they note his unusual talent for helping fellow students, and later his own students, in understanding their own ideas and yet refused co–authorship for any papers he had worked on. Their own comments suggest how much wider his influence was than citation counts suggest:

> Cullen hardly ever accepted co–authorship of publications, but the acknowledgements sections of key papers published between the mid 1950s and 1980s show the breadth and depth of his influence, as do the career successes of his students. He was the kind of academic that would be pruned out in the contemporary publish–or–perish, environment in universities. But if he had followed what is now a common practice of putting his name on all the papers of his students and co–workers that he had helped he would have stood out as one of the most prolific ethologists of his time. (Krebs & Dawkins, 2001:704)

were the blackheaded gulls studied by Martin Moynihan. His laboratory work on pilchards was on the problem of how to record and measure schooling behaviour. Schooling is where sticklebacks (and many other fish species) space themselves in three dimensions in physical groupings. Ethologists faced considerable difficulty in measuring schooling. Judging nesting distances, or animal territories on land or on cliffs is relatively easy, as they are stationary and can therefore be conveniently measured. The opposite is true of a fish–school, which is composed of constantly moving fish, who are reacting to each other, and to stimuli external to the school. Measuring nest proximity on a sand–dune risks angry seagull attacks and the associated mess, but measuring schooling requires intellectually much more sophisticated models and techniques. The Tinbergians were well placed to tackle this phenomenon, however, because of the standard practices of their behaviour laboratory. This is due at least in part to the extraordinarily close observation style that I described above in the work by Desmond Morris, monitoring movement by movement the whole of a stickleback courtship sequence, something that Cullen did with pilchards as well.

Cullen's work on fish schooling sought to understand and describe the structure of pilchard schools. Even though his published papers were primarily concerned with methodological issues, Cullen's evident interest in their behaviour, and his concerns about the limitations of the laboratory as a study space, follow classic Tinbergian patterns:

> A number of workers have found that schooling behaviour is often disturbed in aquaria though the reasons for this are not altogether understood. We found the same, particularly for groups of pilchards that which had been some days in the laboratory. They spent much of their time swimming round and round in tight circles, the “milling” of Parr (1927), Breder (1951,1959) and others.[130] This milling is seen in the sea also, but becomes more frequent in the aquaria. (Cullen, et al. 1965:5)

130The papers referred to here: Breder, (1951, 1959); and Parr (1927) are are all in the bibliography.

All animal researchers are interested to a certain extent in the relationship between the laboratory condition and the animals under study, however it was a special concern for Cullen and other Tinbergians as their raison d'être was the study of natural behaviour. Pilchards were perhaps not a "natural" laboratory animal, and though their schooling was what made the study of their behaviour worthwhile and interesting, it also presented unique challenges. Burian (1993) made the case that the choice of experimental animal mattered profoundly for the epistemological outcomes of the experiments performed with them. He states:

> The value of an organism as an experimental tool, or in field studies, depends not only on various features of the organism but also on the problems to be addressed and the available experimental and field techniques. Indeed, even when some organism is "the" right one for a theoretical job, its rightness is temporary and more or less local or regional. It depends not only on the job, but also on the techniques employed and the social or institutional support system for doing that job. (Burian, 1993:352)

This was definitely the case for Cullen's work, as he had an interesting behavioural phenomenon to investigate, but in the process of investigating an animal that was not a 'traditional' laboratory companion there were certainly unique difficulties, the most important one being the risk of the fish merely "milling" around and not exhibiting the prized natural schooling behaviour in which the ethologists were interested. Kohler (1993),[131] writing on the history of *Drosophila melanogaster* in the laboratory makes a significant related point that the nature of Drosophila specially fitted them to be a laboratory animal:

> Was it merely an accident that melanogaster was both the first Drosophila to enter the laboratory and the best suited for laboratory life? Perhaps not entirely. Melanogaster had, after all, been cohabiting and adapting to

131 Both Burian and Kohler were writing in the Journal for the History of Biology, in an issue that emerged from an ISHPSSB special session on laboratory animals as 'The right tool for the Job' (Burian & Lederman, 1993), so it is not just a co–incidence that their thoughts turned to similar questions at the same time.

> humankind for some thousands of years. Perhaps there was less difference than we might imagine between the ecology of the laboratory and of the places, outdoors and indoors, where melanogaster had long flourished as a hanger–on of humankind. The very traits that made melanogaster a good hitchhiker were precisely the same traits that made it a good standard laboratory animal. It was hardy and not fastidious about what or where it fed [sic.], and was thus more likely to turn up in drosophilists' traps and to flourish in overcrowded laboratory jars. It was relatively tolerant of heat and cold from following humankind into inclement regions and wintering over in chilly fruit stores and cellars. It was already an indoor creature, accustomed to human habitations and able to brave hostile urban environments. It was the ultimate successful opportunist. Cosmopolitan species, in short, were pre–adapted to laboratory life, and D. melanogaster was the cosmopolitan fly par excellence. It had been shaped by natural selection to live in a commensal relationship with humankind. It was the most likely to turn up on a window ledge or in a trap. The forces that made melanogaster such a successful cosmopolitan and camp follower of the most cosmopolitan of primates, also suited it well to a symbiotic relationship with the variety of humankind who inhabit experimental laboratories. (Kohler, 1993:310)

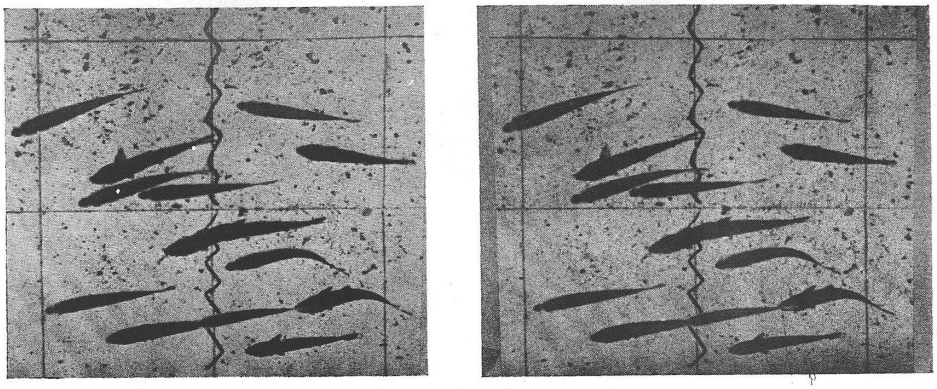
Almost the opposite could be written about appropriateness of the pilchard to be a laboratory denizen, as it is a wild seawater fish, normally found in large schools and accustomed to open waters. Cullen hints at the difficulties of studying wild behaviour when he states that the best results were on fish recently caught and observed in a large tank, in which schooling occurred for the first few hours (Cullen et al, 1965:534) before their behaviour drifts into the “milling” about which did not interest the Tinbergians. In the crucial window before the pilchards began milling, Cullen took a series of Stereo photographs from stands above the tank and measured the distances between the fish in each picture, and between the fish and a known fixed grid painted onto the base of the tank. The twin readings from each pair of photographs were then used to ascertain the parallax so as to discover their distance

from the bottom of the tank, from which it is then possible to derive their distance from each other in three dimensions, something that a single flat photograph cannot show. Cullen shows how below:

[Image 11] (Cullen et al. 1965:536)

CULLEN *et al.*: MEASURING THE STRUCTURE OF FISH SCHOOLS

PLATE V



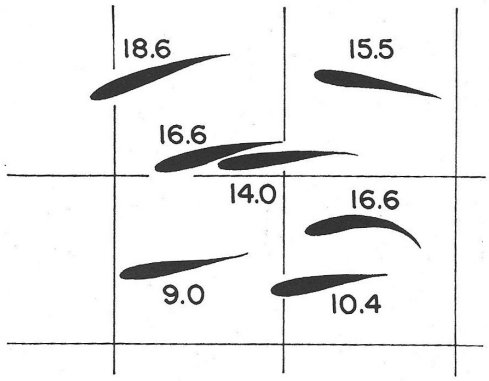


Fig. 1. Typical pair of twin stereo photographs of school of pilchards. The drawing indicates the positions of the individual fish and their height above the bottom in centimetres as calculated from the parallax. In this method the shadows cast by the fish are irrelevant.

The two photographs and one diagram shown above are is not a conventional Tinbergian images, but rather tools for fish geometry. In this respect it is a break from Morris's 'behaviour only' type of diagrams. However that it exist at all is because of a concern with understanding behaviour as an end in itself, something that he shares with Morris. The composite diagram that Cullen drew below the two photographs, using each of them to derive the fish's individual parallaxes takes a physical–geographic approach to the study of a behaviour. In its appearance and informational content it is different to Morris's later diagrams, but it remains closer to

the Tinbergian tradition than to the kind of mathematical work done by fellow ichthyologists, like Hynes. What ties together Cullen's and Morris's type of work, and differentiates it from the other ichthyologists is that Cullen's work focusses on the spatial dimensions of behaviour. It may be that Morris's images had consciously influenced Cullen's – but much more significant was the influence of Morris (and Tinbergen's) interest in studying the behaviour of fish by closely observing them.

There are qualitative differences between Cullen's approach and that of his ichthyological contemporaries in both method and representation. His use of diagrams of the fish themselves is quite unusual, as much of the research on schooling of the period made little use of them. For example Cushing and Harden–Jones (1968) in a paper titled 'Why do Fish School,' have only equations other than their standard text, even though they state that 'Studies of fish behaviour suggest that the habit of schooling, whatever its mechanism is of advantage to prey.' This suggests that even where his contemporaries were considering behaviour, they were not interested in representing it, or using diagrams to understand it. Cushing and Harden–Jones study their pilchards' schooling behaviour out at sea, and make use of technology in order to make this monitoring possible: 'As fisheries biologists, we work on this problem in the open sea or in the deep ocean with acoustic equipment' (Cushing & Hayden–Jones, 1968:918). This again sets them apart from the trends of the early Tinbergians, who were always more concerned with what they could see and record directly, than what could be recorded by automatic or technological monitoring.

Here, then is an unusual case, where given the choice of studying a behaviour in nature or in the laboratory the Tinbergian chose the laboratory and his scholarly rivals went to the field (or in this case the open ocean). Cullen chose to bring open-water sea fish into the laboratory to study their behaviour until such a point where they became accustomed to the laboratory (institutionalised?) and no longer performed. This shows the adaptability of the Tinbergian approach, but it also suggests that they valued *direct observation of behaviour* even above their commitment to fieldwork. Cullen had done his D.Phil. research in the field, on the

Farne Islands on arctic terns, (1956), but nevertheless he chose when studying pilchards to directly observe behaviour rather than go into the field (or in this case out to sea) and monitor it remotely via acoustic soundings as Cushing and Hayden–Jones had done.

The Tinbergian laboratory then was a place that drew nature and natural behaviour into itself. It existed for the direct observation of behaviour – 'fishwatching' – in Morris's (1979:74) marvellous phrase, and maintained this ideal even where there was the option to go into the field and monitor remotely.

Section 2: Exchange between laboratory and field

Understanding natural behaviour was what the Tinbergians were for. Their focus on natural behaviour bound together their laboratory and field observations and research, as they treated 'natural behaviour' as a unified object that could be studied under various conditions. The physical context of the research was left in the background and observations of 'individual behaviours' as phenomena in themselves were what became significant as objects of study. This held to such an extent that even in output on gulls, laboratory sticklebacks turn up, and conversely apparently field–derived theories like displacement activities turn up in laboratory research. What I will explore in this section is the interaction between the two sites of research, and how the currency of natural behaviour served to unify them.

Section 2.1 Naturalising the Laboratory in practice and observation style

One of the characteristics of the Tinbergen laboratory that stands out most clearly is the determination to 'naturalise' the laboratory as far as was possible. They endeavoured to naturalise the surroundings that the fish themselves lived in, in order that in its turn their behaviour would be near to natural. This included using as large a set of tanks as was practical, filling them with weeds, and as far as possible letting the stickleback perform as they would naturally perform. A sense of the way that they

taught themselves not to see the laboratory, but instead to focus on the behaviour can be gleaned from this description by Morris of what he observed during the breeding season:

> With the arrival of the breeding season, male, ten–spined sticklebacks cease to swim in shoals and begin to space themselves out among the water–weeds, each one defending a territory against the others. Their bodies become jet black in colour and they start to construct a small nest of plant filaments, lodged carefully in a clump of weeds. They bore a tunnel into this nest and then start to look for a ripe female, swollen with eggs. On seeing her, they perform a vigorous head–down dance, zig–zagging their way slowly towards the nest–site. If the female is nearly ready to lay her eggs, she follows closely behind the dancing male and pushes her nose into the entrance. The male hovers above her, pointing to the nest entrance with his nose. If she then enters the nest and lies quietly in the tunnel, he moves down a little and begins to shiver his nose against her protruding tail. If she leaves the nest by the tunnel exit without laying her eggs, he then pursues her and bites her savagely, before starting to court again. If, on the other hand, she lays her eggs in the nest before leaving, the male then follows her quickly through the tunnel and fertilizes the eggs. After this, he guards and cares for the eggs day after day until they hatch, the liberated female stickleback taking no further interest in her offspring. (Morris, 1979: 77–8)

This vivid description leaves us with a very graphic image of the courtship behaviour of the ten–spined stickleback. The focus is so minutely on the behaviour of the animals that we never notice the laboratory context. To take a comparison with work from Morris's Behaviorist contemporaries we can see exactly how the laboratory can be present in research description:

> SUMMARY AND CONCLUSIONS
>
> This experiment was designed to find out if a learned response continues

> to be made after satiation of the relevant drive under which it is being or has been developed. The Ss of the experiment were 84 albino rats, ranging in age from 90 to 120 days. All Ss were trained in a single–unit T–maze, with food designating the correct side. They were given four training trials daily; furthermore, they were run each day immediately after feeding, to check on the strength of the habit in the absence of the relevant drive. Forced trials were employed to make sure that all Ss ran an equal number of trials to both the correct and incorrect sides of the maze. (Teel and Webb, 1950:151).[132]

The presence of the laboratory here is overwhelming– the rats are described as Ss (subjects), trained and put through forced trials in a manner of constant intervention and with the idea of studying how much their behaviour can be modified. The comparison is worthwhile precisely because it highlights how different the Tinbergian approach was at this period. The difference in language is substantial as we can see from Morris's article:

> The area around the nest site is patrolled and defended by the male owner, other fish, particularly males of the same species, being driven away. Normally there are a number of such territories together in a stretch of weed in the stream. At the beginning of the season the boundaries are not clearly defined, and males are constantly trespassing into one another's nesting areas and a considerable amount of fighting ensues. Gradually the boundaries become more clearly defined, and correlated with this there is less actual fighting and more threatening.

132Teel and Webb were conventional rat–maze psychologists following much of B.F. Skinner's approach and methodology, they were using a Skinner box, for their research.

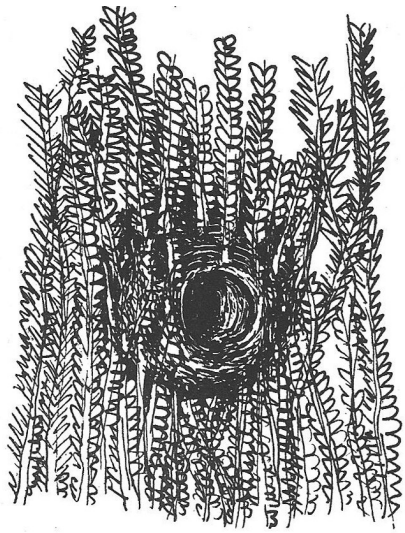


Fig. 1. The Nest of the Ten-Spined Stickleback.

[Image inserted is 12]

> When the females are ripe they swim through the territories and are courted by those males which are ready to fertilise. If the females do not respond to the courting males in a certain manner, they, like other males are attacked also. So the area around the nest of a male is forbidden ground to all fish save a female which is ready to lay eggs. (Morris, 1951:234)

Morris's description has the air of a field observation, there is the diagram of the fish's nest amongst the weeds which has the air of the purest observations of the old–fashioned naturalist. Above and below this picture the text adds to the way that this feeling is conveyed, fish 'patrol', 'trespass', and 'court' all of which is very active language, which again helps to situate them as behaving naturally in their natural environment. Although he later notes that the observations were done in the laboratory, the difference in overall impression between Morris's writing and that of the 'rat–maze' psychologists whom the Tinbergians so derided is almost insurmountably large. By contrast, there is evident kinship with both the style and content of their field colleagues' work. Moynihan's drawings for example very often include similar levels of contextual detail to that above, as do his descriptions of behaviour. Moynihan here is describing a menacing song by a blackheaded gull:

One very pronounced, easily recognizable, individual variant of the Long Call seems to be uttered by only a small proportion of birds. Most of the individuals I have heard producing this variant have been juveniles. Their Long Call Notes are softer, rather more melodious than the typical Long Call Notes; and sometimes show slight indications of a trisyllabic division.

The aerial Long Call and Long Call Note are not necessarily accompanied by any specific postures or movements. A flying gull sometimes produces these calls suddenly, without any other apparent alteration in behaviour, and without ceasing to fly in a perfectly typical, "relaxed," fashion. At other times, however, a flying gull may go into the posture shown in Pl.1 fig A [image 13], when it produces the Long Call Note or (more frequently) the Long Call. This posture differs from the typical flying posture in several respects. The head and neck, instead of being "pulled–in", as they would be during typical flying, are stretched forward and slightly upward. Moreover, the breast and belly seem unusually prominent. (This latter effect is presumably the simple result of the stretching of the neck.)

Plate 1. Pursuit Flight postures of the Black-headed Gull.
Figure A, left. Posture from which the aerial Long Call is given.
Figure B, right. "Hanging" posture after a shallow Soar.

[Image inserted is 13]

> It should be mentioned that this rather peculiar posture, from which a flying gull may utter the Long Call is slightly reminiscent of the Oblique Posture, from which a gull on the ground or water utters the Long Call. (Moynihan, 1954: 31–32).

Both Moynihan's language and his choice of diagram are akin to those used by Morris. Moynihan's suggestion that the juvenile's song is more 'melodious' and that at certain points they can be seen to be 'relaxed', and his line drawing a little chimes with the nest, and very much more so both with Morris's behavioural diagram (image 3.6) and also with the activity that is present in Tinbergen's 'dancing' fish diagrams.

Section 2.2 Images and Ideas moving between laboratory and field

The Study of Instinct (1951) a book which had a great deal of fieldwork and field science in it, and which made great use of Tinbergen's work on gulls, nevertheless had as its frontispiece a laboratory stickleback dancing at its reflection in a mirror:

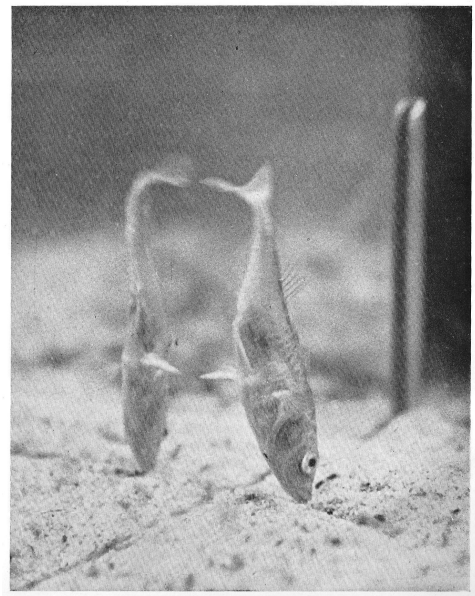


FIG. 1. Male Three-spined Stickleback (*Gasterosteus aculeatus*) in threat posture in front of mirror. This activity is innate (p. 51), dependent on internal (motivational, p. 63) and external (sensory, p. 28) factors. It has an intimidating effect on other males of the same species (p. 177). Historically, it is displacement sand-digging (p. 113), changed by ritualization (p. 184)

[Image 14] (Tinbergen, 1951: frontispiece)

Further into the book, Tinbergen's 'dancing' diagrams showed in visual form

something of the courtship patterns that Morris was also trying to describe. [133] The difficulty of representing three dimensional motion with both accuracy and a sense of life is an inherent representational challenge of any behavioural diagram, but Tinbergen's do show us those aspects of the courtship ritual that he wants us to note. The second diagram in the pair could be written as one of Morris's behavioural sequences, or as a pattern of stimulus and response from male and female sticklebacks. Its being represented with arrows and positioned directly below the behavioural diagram though means that we read it not as a set of words, but as a series of stages in a three dimensional behavioural process. What being diagrammatically represented does to the words is to give them a sense of 'flow' so that they seem to be less a series of labels, and more a depiction of behaviour, that happens to use words:

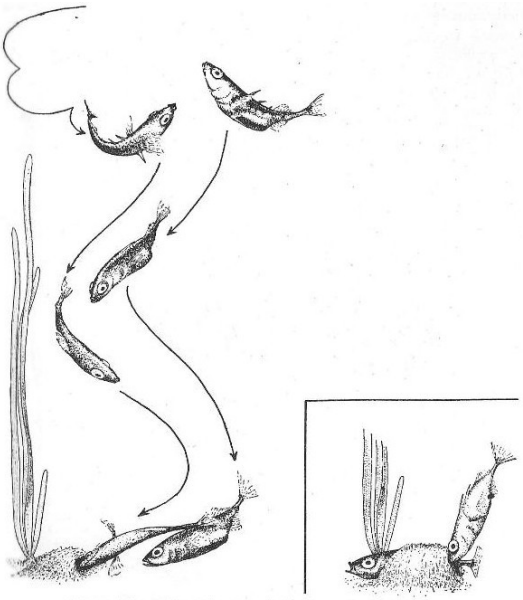


FIG. 47. The mating behaviour of the three-spined stickleback.

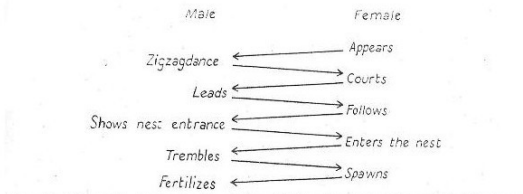


FIG. 48. Schematic representation of the relations between male and female three-spined stickleback. After Tinbergen, 1942.

5291 E

133Having showed these diagrams at several lectures I have given, the most common response of the audience members has been to liken them to the kind of 'step pattern' sheets that you can get to learn to dance. The sense of life and vivacity that these diagrams convey I think is very similar, but so to is the challenge of representing movement on what is a fixed medium, so it is perhaps unsurprising that the two are similar.

[Image 15] (Tinbergen, 1951: 49)

This pair of images almost perfectly mask their own context. The "site" of the research has been entirely lost, and without careful checking one would assume that this was observation of natural behaviour and there is nothing to suggest that it occurred and was observed under laboratory conditions. The more explicitly analytical lower diagram moves from observation to analysis without pause for physical context. Its presence directs the eye to see the higher diagram as though it were explaining the features of it, however we are instead reading them back into the original diagram, a process described by Mike Lynch's work, in which he calls these kinds of paired scientific images 'eidetic images' (Lynch 1988:210).[134]

When images and observations moved between laboratory and field, they took meanings and ideas with them. The most stark example of this comes from The Herring Gull's World (1953b) which in spite of its title uses observations, diagrams, and ideas developed on laboratory sticklebacks, to make sense of seemingly mysterious gull behaviours. The clearest instance of this comes from when Tinbergen was trying to elucidate why herring gull's perform 'grass–pulling' during fights, an observable behaviour apparently of no value to either participant. He shows it thus:

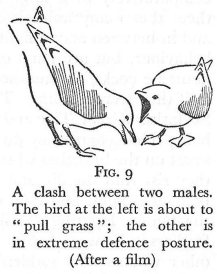


FIG. 9
A clash between two males. The bird at the left is about to "pull grass"; the other is in extreme defence posture. (After a film)

[Image 16] (Tinbergen, 1953b:65)[135]

To understand the behaviour observed, Tinbergen made use of the idea of 'Displacement activities'. The notion of 'displacement activities' was amongst Tinbergen's most powerful theoretical tools, a way for understanding previously

134Lynch's work on scientific illustration, particularly on the 'eidetic image' is complex, as he argues that apparently 'simplified' diagrams are laden with meaning and have the effect of returning one's eye to the 'original' or more complicated version, and *seeing* in it the features that the 'simplified' diagram emphasises. (See Lynch 1985, 1988; with Woolgar 1988).

135This is clearly an instance where Tinbergen did make the diagram from the film, but as I stated above, this is by no means the rule, as there are both many diagrams without the attribution of the original to a film or to a photograph.

incomprehensible behaviour patterns such as grass–pulling here. The sudden occurrence of 'out of place' behaviour in moments of great stress Tinbergen explained occurred because of conflict between different drives, such as the drive to flee and the drive to fight. To explain this then novel idea to the readers of The Herring Gull's World (1953b), however he introduced his laboratory research on sticklebacks, and their displacement activities. He even begins with a line drawing reproduction of the same picture of the stickleback from the frontispiece of The Study of Instinct, (1951):

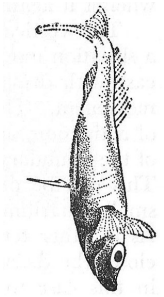


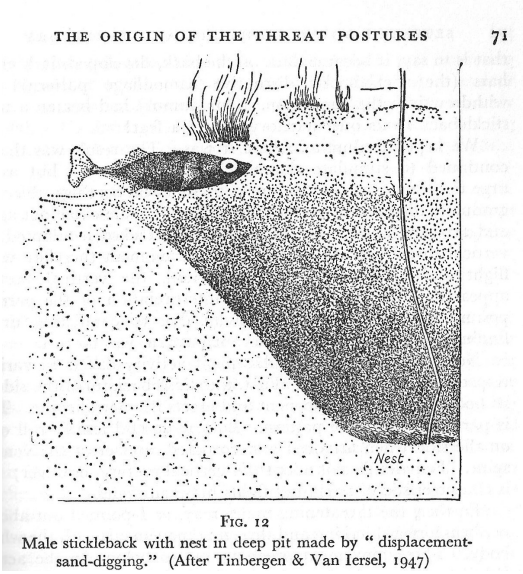
FIG. 11
Threat posture of male Three-spined Stickleback. (After a photograph in Tinbergen, 1951)

[Image 17] (Tinbergen, 1953b:69)

This use of a stickleback diagram in a book on herring gulls for general audience is quite strange, or at least out–of–place. The Herring Gulls World was for the New Naturalist series, which were aimed at a lay audience who could not be expected to have access to a laboratory, but would be expected to go out and observe and interact with their subjects. Partly it was because the stickleback observations were his exemplar case so far as displacement activities were concerned, so it coloured his own thinking on the subject to such an extent that using another example may have seemed either difficult or less explanatory. Partly it is also that he wanted to convince the audience of bird-lovers who were buying and reading The Herring Gulls World of the value of studies on animals.[136] Finally it is an immediately understandable example, so is ideal for use as a heuristic, particularly when he showed some of the context. Tinbergen demonstrated the practical consequences of displacement

136Tinbergen frequently remarked on how narrow British amateurs were in their choice of species, being bird watchers, aquaria fans and so on, with a lack of interest in 'general natural history', a point he made to W.H. Thorpe (Thorpe, 1979)

behaviour in the next diagram, also of a stickleback, in which he depicted the creation of a sunken sand nest:



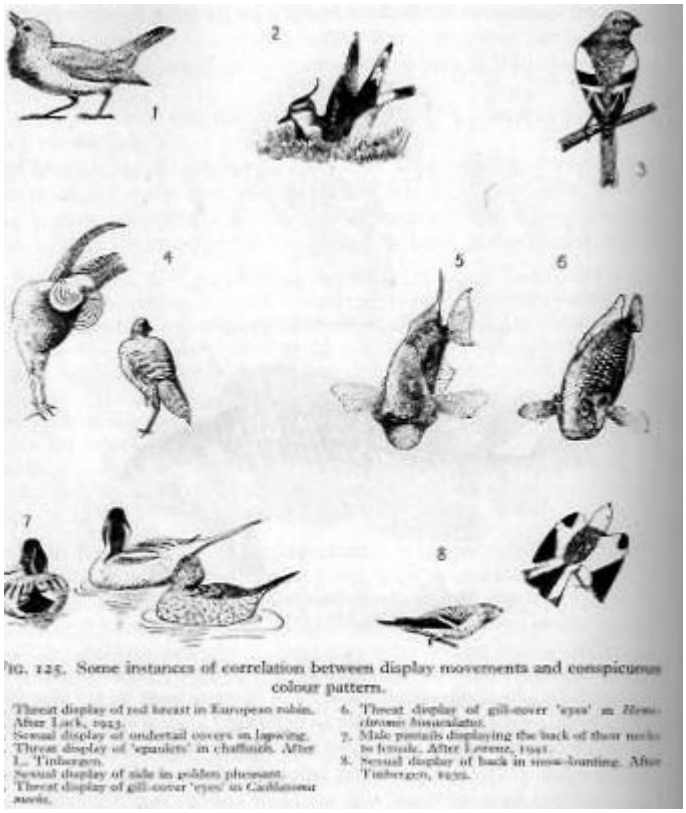
[Image 18] (Tinbergen, 1953b:71)

The sunken nest is, in this instance the example par excellence of the out–of–control displacement behaviour, the nest would normally be only a small hole, but as a consequence of constant stress and conflict, the stickleback's nervous digging results in a substantial pit. After a lengthy explanation of the behaviour in sticklebacks, Tinbergen then asks for understanding in his use of fish materials, begging the excuse that there is much to be learned from applying research on the behaviour of one species to another:

> I hope the ornithological reader will not be annoyed by this rather lengthy narrative of the behaviour of a mere fish. I cannot promise that I will not deviate from the ornithological path in this book again. In ethology, comparison is too powerful a tool to be neglected. The bird student may acquire a better insight in his birds by studying a fish or even an insect; conversely, the study of bird behaviour may help us in understanding the behaviour of other creatures, man included. As a matter of fact, the student of animal behaviour finds himself continuously applying his findings to his own species, and, without entering into details, I must confess that much of what little understanding I have of

> human nature has been derived not only from man–watching, but from birdwatching and fish–watching as well. It is as if the animals are continuously holding a mirror in front of the observer, and it must be said that the reflection, if properly understood, is often rather embarrassing... (Tinbergen, 1953b:73).

One of the results of this catholic taste for species is that Tinbergen was happy to include stickleback examples in bird centred works, and in otherwise ornithological diagrams such this one below:



IG. 125. Some instances of correlation between display movements and conspicuous colour pattern.

1. Threat display of red breast in European robin. After Lack, 1943.
2. Sexual display of undertail covers in lapwing.
3. Threat display of 'epaulets' in chaffinch. After L. Tinbergen.
4. Sexual display of side in golden pheasant.
5. Threat display of gill-cover 'eyes' in Cichlasoma nuchs.
6. Threat display of gill-cover 'eyes' in Hemichromis bimaculatus.
7. Male pintails displaying the back of their necks to female. After Lorenz, 1941.
8. Sexual display of back in snow-bunting. After Tinbergen, 1939.

[Image 19] (Tinbergen, 1951:115)

This image, of a type of behaviour – the displacement activity – shows this type behaviour in many species. Alongside the gulls above, there are game and fowl, and most oddly, at position 5, a lone stickleback. Though sticklebacks are only extremely distantly related to birds, Tinbergen clearly felt he had observed a 'homologous' behaviour pattern in the fish.

The image itself is from The Study of Instinct, (1951) which did cover the behaviour of many species, but that should not let the the strangeness of it escape us, that amongst a battery of images of bird behaviour there are some of Tinbergen's cichlids. This should remind us once again that the primary subject of the school is *behaviour*, rather than a species, even purely ornithology. The 'displacement activity' was a category of behaviour that Tinbergen took much of the credit for discovering, and which was cited as being amongst his most important innovations in hie Nobel commendation. What is so unique about this behaviour is that it is not a characteristic of any individual species, or indeed even class or order of species, but rather displacement activities broadly fitting his definition were observed by his students (and others) across species, (as was mentioned in the previous section) and across physical locations. The clearest statement of what he means by a displacement activity in this early period comes from The Study of Instinct (1951):

> It has struck many observers that animals may, under certain circumstances, perform movements which do not belong to the motor pattern of the instinct that is activated at the moment of observation. For instance, fighting domestic cocks may suddenly pick at the ground, as if they were feeding. Fighting European starlings may vigorously preen their feathers. Courting birds of paradise wipe their bills now and then. Herring gulls, while engaged in deadly combat, may all at once pluck nesting material, &c. (Tinbergen, 1951: 114)

Following this description Tinbergen inserts image 19 (above) deliberately to show the diversity of anomalous behaviours that he feels will be understood through this new framework. From the perspective of research places it is interesting to see his examples: there is the domesticated cock, studied at home; the European starling, which is predominantly a garden bird; and the herring gull, which is studied in field on the dunes. Even more exotic is the bird of paradise, which must be studied in its habitat in the jungles of East Asia or Australia. That displacement activities were observed in these different places and under such varying conditions– domestication, the near outdoors, the edges of the country, and in distant lands, suggests the

explanatory adaptability of the theory, and so it should not surprise us that it traversed relatively freely the boundary between laboratory and field. In order to explain the idea of a displacement activity in the first place to his ornithological audience in The Herring Gull's World, (1953), as we saw above, he chose to use an example not from his ornithological work, but from the laboratory observations on stickleback.[137] Tinbergen's willingness to apply observations of many species, from very varied places, and studied under very different conditions was profound, and in the idea of 'displacement activities' he had a theory that could be applied equally to laboratory and field observation. Along with the idea of the Innate Releasing Mechanism,[138] for which, almost perversely the idea of the displacement activity

137When he moved to a more specific level, looking to explain displacement activities in herring gulls Tinbergen applied a similar approach. He listed field observations of displacement activities similar to those seen in herring gulls that had been reported on a large variety of other birds:

> The peculiar behaviour of gulls threatening each other becomes more intelligible when threat–behaviour is studied comparatively in a large number of species. It will be seen then, that many animals occasionally perform activities during and in between actual fights that "don't belong" to the fighting behaviour, but are parts of other behaviour–patterns. Fighting domestic cocks, for instance, peck at the ground now and then as if they were feeding. The same can be seen in fighting male Skylarks. Great Tits and Blue Tits do the same, except that, being tree feeders, they do not peck at the ground but tear buds apart on the branches where their fighting is done. Alternatively they rise into the air and attack each other in a typical, steep, bouncing flight, and then settle on twigs and peck vigorously at the buds. Fighting starlings and fighting Cranes preen their feathers in between fights. Fighting Avocets, Oystercatchers and other waders may suddenly turn the head round, put the bill under the scapulars and act as if they were going to sleep! There are many other instances known (Armstrong, 1950; Kortlandt, 1940; Tinbergen, 1939, 1940, 1952). Feeding, preening, nesting behaviour, or even sleep, are suddenly shown when the whole situation seems to dictate nothing but fighting. (Tinbergen, 1953b:65–66)

138IRMs (and in Konrad Lorenz's original phrase, innate perceptory mechanisms) were at the heart of the early school's work, and were an idea that was also strongly linked with Tinbergen's relationship with Lorenz. Lorenz suggested the idea of the releaser in his ground–breaking 1935 'Kumpan' papers, translated and abridged into English in 1937. Lorenz's idea likened complicated behavioural responses to finding keys for specific locks, which then 'released' the behavioural mechanism:

> 'It is an old but fitting metaphor to liken the releasing set of stimuli to the key, and the innate perceptory pattern to the lock of the instinctive reaction. Even more appropriate, is the simile of a combination lock that cannot be opened except by a definite series of manipulations which, by reason of their general improbability, it is practically impossible to find by chance. The relation of the particular form of the lock to the key that fits it, or of any innate perceptory pattern to the set of stimuli to which it responds, is ever a compromise between greatest possible simplicity and greatest possible general improbability. The improbability of the innate perceptory pattern is to guard the instinctive reaction from being released by chance through other than the biologically 'right' influences. Surprisingly simple though the innate perceptory patterns are in the three cases cited as examples, they are evidently efficient enough, when natural conditions are taken for granted, to prevent the 'erroneous' unlocking of the reaction.' (Lorenz, 1937: 247–248)

Lorenz's idea was profoundly influential over the Tinbergians. Its clarity provided it with great accessibility, and also wide possibilities for applicability. Lorenz himself specialised on

became one of the prime exemplars, they were the Tinbergians raison d'être.

domesticated animals such as geese and ducks but the Tinbergians took his idea both into the wild, and also into their laboratory.

Conclusion: Watching Nature in the Laboratory

The main themes of this chapter have been the investigation of the Tinbergian laboratory, both in relation to its subject of study and its outputs, on the one hand; and on the other its relationship with the fieldworkers of the Tinbergians and to an extent the wider world. In the first section I sought to situate the Tinbergian laboratory as a central part of the Tinbergians, producing theoretical and experimental work such as Margaret Bastock's observations, which brought together the work of the Tinbergians on observing animal behaviour along with the classic Drosophila work of the modern synthesis. I also explained the work of one of Tinbergen's most famous students, Desmond Morris, on sticklebacks, which showed how hard Tinbergen worked to try to bring an intense close observation style as well as bringing the ethos of the field, with all its austerities, discomforts and deprivations, into the laboratory. Along with that I showed how profoundly different the Tinbergians' research was from fellow behaviour researchers based both in the laboratory and in the field.

Cullen's laboratory complex work on fish trigonometry demonstrated the extent to which the Tinbergian observation style could be stretched, with Cullen's heavily mathematical basis built only after close observation of pilchard behaviour, and only to answer questions about behaviour. This I contrasted to Cullen's contemporaries in the field of schooling in ichthyology for whom the use of direct observations were rare, and whose focus was on highly technologised solutions. Cullen's later work provided us an interesting case study as he chose to take pilchards into the laboratory even though they were hardly the 'right tool for the job' in Burian's terms to observe their behaviour directly, where his contemporaries often chose to take acoustic equipment (sonar) and investigate them in the open seas. This suggested that it was direct observation that was most valued by the Tinbergians in preference to the naturalism of the surroundings.

The second half of the chapter investigated exchange between laboratory and field in

the early school. It looked at three dimensions of this, showing how this was done in terms both of attempting to naturalise the laboratory, but also the style of observation and representation that was done there. I showed examples both descriptive and visual of how the laboratory site was absented from the way that the Tinbergians presented their findings to the world, to such an extent that unless the reader was very careful it would have been easy to assume that the reports of behaviours seen in the laboratory were field reports. I contrasted the fieldworkers' reports with those of on the one hand Tinbergian laboratory workers, and on the other hand writings from non-Tinbergian laboratories, demonstrating that there were far more, and far more substantial similarities between the two groups of Tinbergians than there were between the two groups of laboratory workers.

I then moved on to show how visual representations and their associated meanings and ideas were applied from one area of the schools research into another, particularly taking the example of research done on sticklebacks that was used to explain observations in herring gulls to an ornithological audience. I then showed that the idea behind the diagrams was the idea of 'displacement activities'. These activities were a category of behaviour that is primarily identified as being one of Tinbergen's great contributions to behavioural sciences. What I showed was interesting about them is that they were ideal examples of natural behaviour objects for the Tinbergians as once one had seen one in one species, any number of behaviours could then be identified as displacement activities in any species under either laboratory or natural circumstances.

Displacement activities provided us with a way into considering the relationship between the laboratory workers and their field colleagues. We saw the high level of inter–species and inter–space transition, with the Tinbergians almost promiscuous in their application of their theories. The principal reason that the Tinbergians felt that they could use their ideas and observations in such a direct trans-species, and trans-local way was because they felt that they were studying the same principal object – the *natural behaviour* of animals – and so considerations of place and or worries about applying studies from one species onto another were considered secondary.

Because they had spent so much time and effort to naturalise the laboratory, as we saw in Morris's writing in the first section, they claimed that the behaviours they were studying were themselves natural; that was after all the point of naturalising the laboratory in the first place. Since they felt they were studying natural behaviour, it made perfect sense to use the same ideas and the same language as their field colleagues and even for their laboratory studies to be re-used by field colleagues as happened in Tinbergen's use of fish diagrams and ideas in herring gull work. Indeed even Margaret Bastock, who experimented with *Drosophila melanogaster* was studying innate behaviour differences, and ergo natural behaviour, by applying Tinbergian close observation to a territory (in in *D. melanogaster* a species) more normally possessed by geneticists. The study of natural behaviour continued to be the focus of Tinbergian studies for years after the early period. How the laboratory workers and fieldworkers practices and ideas changed over time will be the subject of the next chapter as we examine the work of the later school, both in the laboratory and the field, and continue to examine the relationship between the two.

Chapter Four: The later Tinbergians in laboratory and field

Introduction: In search of the adaptationists

The reader may have been surprised that one of the genuinely revolutionary aspects of the Tinbergians, namely the study of behavioural adaptation, has until this point been barely mentioned. The importance of evolutionary work has also been somewhat distant from the main themes of the previous chapters, reflecting the lack of direct interest in it in the early years of the school. Certainly in respect of the idea of evolution there are important interests that stretch back to the very birth of ethology, however the study of adaptations was not a key concern in the very early years of the school. Adaptation became much more central, particularly following Esther Cullen's study of kittiwakes. Cullen's study has been much trailed earlier in the thesis, and much discussed in the secondary literature as well, partly because it shows a quite clear change of direction in the fieldwork that they themselves undertook – though I will also suggest here that it can be best understood in context.f

That the Tinbergians achieved both scientific, and for some popular, acclaim was due partly to this mature period of the school. The Tinbergians lasting impact however was secured by its students, both of the early Hard Core, and also of the post–Esther Cullen generations including Tinbergen's later biographer Hans Kruuk, and a young Richard Dawkins. These two were far from Tinbergen's only later students, however, and the school thrived throughout the 1960s producing high quality students and theoretical work. As well as the injection of adaptation as a theoretical tool following Esther Cullen's work, there were other changes of experimental practice, methodology and theory. One was suggested in the previous chapter with the intriguing cross–overs between laboratory and field, a theme that will also be central in this chapter. The changing nature of field experiments in particular will be a theme of this chapter, looking at the increasingly interventionist approaches that the Tinbergians began to take, and the changing content of those experiments.

Section 1: Watching nature in the later field school

The Tinbergians in the field changed surprisingly rapidly from the high–water mark of observation–led work with Martin Moynihan through the new evolutionary work of Esther Cullen, and into a quite different set of approaches by the mid 1960s. There was a turnover of personnel in this period too, as would be expected of any academic department. Many of the earliest Tinbergians moved on, Robert Hinde to Cambridge, Moynihan himself back to the U.S.A. and eventually onto the Smithsonian Tropical Research Institute in Barro Colorado, Panama; and Desmond Morris, first to London Zoo, and later into more broadly 'media work'. Throughout this period Mike Cullen remained in Oxford, though switching from fieldwork to the kind of laboratory studies that were discussed in the previous chapter. New arrivals in the group included Hans Kruuk Honorary Professor of Animal Behaviour at Aberdeen University; Colin Beer now Professor of Psychology at Rutgers University; Marian Dawkins, currently the head of the ABRG; and Richard Dawkins, whose work I will discuss in a later section. New locations for field research were begun as well, with a shift from the early research sites at Scolthead Island and out to Ravenglass and later Walney in Cumbria. One other place that retained its early significance were the Farne Islands which had a very large kittiwake colony.

Section 1.1 Esther Cullen and adaptation to the cliffs

It is on the Farne Islands that I will begin this section, looking particularly at the work of Esther Cullen. Cullen may seem out–of–place in this section, as she was a member of the Hard Core, and began her research in 1952, but I have included her here as she was such a figure of change that I feel she fits the section better. She arrived after Hinde had moved on to Cambridge, and when Moynihan had already been in Oxford (or in the field) for two years. Esther Cullen's work took a radically different turn from that of any of the figures I have previously introduced, although like most earlier research it was founded on direct observations. There are also historiographical reasons for focusing in on Esther Cullen at this point. Both Kruuk

(2003: 169–179), and in more depth Burkhardt (2005:414–421) highlight her work as being of considerable importance, and Burkhardt suggests that Cullen's 'discoveries played a critical role in Tinbergen's sense of metamorphosis in the mid–1950s' (Burkhardt, 2005:417). Kruuk situates Esther Cullen in the Hard Core, but Burkhardt's characterisation of her work as a key part in the changing nature of the group is more insightful.

Cullen's work was based on a very close observation of kittiwake life, made by her of kittiwakes on the steep cliffs of the Farne Islands, and in it she discovered significant differences between the behaviour of the members of the gull family that had previously been studied by the Tinbergians, and those which she was herself studying. The herring gull, Tinbergen's great love, and the blackheaded gull, studied so intensely by Martin Moynihan are both ground–nesting birds, and have quite similar behaviour patterns, especially when compared, as they were by Esther Cullen, to the kittiwake. Cullen's lengthy comparison introduced a new emphasis on behavioural adaptation due to evolution, to explain behaviour. This contrasts with Martin Moynihan's work which I investigated in the previous chapter in which this level of explanation was deliberately left absent. Where Moynihan bracketed off explanatory analysis at any level beyond investigating the immediate stimulus or environmental context, Cullen's work launched an almost fully formed adaptationist understanding of the behaviours she observed, as is evident in the following lengthy quote:

> The Kittiwake is probably derived from a ground–nesting gull and the change to cliff–nesting was presumably an anti–predator device. Because predation is less, the species seems to have lost a number of behaviour patterns and morphological features possessed by other gulls. On the other hand it has had to acquire a number of adaptations to suit its new life. Signal and non–signal movements have been altered: some have been modified, like the beak hiding or the nest–building movements, other have been lost, like several anti–predator devices or the aggressive upright posture. There also seem to be a few new acquisitions like the

black neck–band of the young and the collecting of mud.

Adaptations to fit an animal for a new kind of life are of two kinds. Some are inherited, others are acquired as a result of the individual's experience and environment. The chief morphological peculiarities of the Kittiwake, such as the black neck–band in the young, are certainly due to inherited differences. The adults claws are sharper than those of other gulls who spend the whole year close to land. On the other hand this difference is also apparent in the newly born young, so that here too it must have a genetic basis.

As I have shown, some of the differences in behaviour also are innate (the presence or absence of head–turning in the young, their readiness to run away when pecked). Others, for instance the use of mud as nest–material, are presumably also innate. Yet others, such as the social collecting of material, may be due to a complicated interaction of acquired and inherited factors. The existence of inherited factors leading to differences in behaviour should not blind one to the possibility that experience may be able to modify a pattern. This was shown in one of my experiments in which a newly–hatched Black–headed Gull learned after a day to take the food from the throat of its Kittiwake foster–parent in the way a young Kittiwake does from the first. Such modifiability is no objection to the existence of innate differences; it only shows that these differences may not be as rigid as has sometimes been supposed.

With the adaptations described in this paper, and which are summarized in the list below, I hope to have shown how this one change to nesting on tiny ledges on steep cliffs has had repercussions in many aspects of the life of the species and has led to morphological changes as well as a great many alterations in behaviour. In many animals adaptive differences between species have been described but I know of no other case where one relatively simple change can be shown to have been responsible for so many alterations.

GROUND-NESTING GULLS	KITTIWAKE
High predation-rate in nesting colonies.	*Predation pressure relaxed on cliffs.*
Alarm-call frequent.	Alarm-call rarer.
Adults leave nest when predator some way distant.	Remain on nest until predator very close.
Vigorously attacks predator intruding in colony.	Very weak attacks at most at intruding predator.
Brooding birds disperse droppings and carry egg-shells away from nest.	Neither droppings nor egg-shells dispersed.
Young cryptic in appearance and behaviour.	Young not cryptic either in appearance or behaviour.
Clutch-size normally three eggs.	Clutch-size normally two eggs.
Suited to life in colony on ground.	*Adapted to life on cliffs.*
A. Several fighting methods.	More specialized to fighting in one way (grabbing beak and twisting).
Upright threat posture occurs, derived from preparation to peck down at opponent.	No upright threat.
Beak does not specially direct attacks. Not known if it is such a strong releasing stimulus as in the Kittiwake.	Beak releases and directs attacks.
Beak turned away in appeasement but not elaborately hidden.	Beak turned away in appeasement and elaborately hidden.
B. Young run away when attacked.	Young do not run when attacked.
No head-flagging in young.	Head-turning and hiding of beak in young when pecked and appropriate behaviour in attacker.
No neck-band.	Possess black neck-band.
C. Number of nest-sites probably less restricted and therefore probably less competition for nest-sites.	Number of nest-sites restricted, probably more competition.
Often first occupy pairing territories before nesting territories and pairs form away from nest.	Occupy nesting ledges at arrival in breeding area and pairs form on the nest.
Choking not normally used by unmated males as advertisement display.	Choking normal advertisement display of unmated males.
D. Copulation on the ground, female stands.	Copulation on the tiny ledge or nest, female sits on tarsi.
E. Nest-material collected near nest, building not synchronised, individual collecting.	Nest-material collected in unfamiliar places, synchronization of building and social collecting.
Little stealing of nest-material.	Birds very ready to steal nest-material.
Nests often unguarded before laying of first egg.	Nests guarded.
Nest-building technique relatively simple.	Nest-building technique more elaborate.
Mud not used.	Mud as nest-material.
Only one or, at most, very short series of depositing jerks.	Prolonged jerking of head when depositing nest-material.
Only traces of trampling on nest-material.	Prolonged trampling on nest-material.
Nest has relatively shallow cup.	Nest has deeper cup.

F. Young leave nest a few days after hatching.	Young have to stay on nest for long period.
Young fed by regurgitation on the ground.	Young fed from throat.
Nest-cleaning absent or less conspicuous.	Young and adults pick up and throw away strange objects falling into nest.
Parents have feeding call, probably to attract young.	Parents have no feeding call.
Hungry young make themselves conspicuous to parents by head-pumping.	Head-pumping absent in young.
Parents learn to recognise own young in a few days.	Parents do not recognize own chicks at least up to the age of four weeks.
G. Young face any direction. Vigorous wing-flapping in young.	Young face wall much of the time. Flight movements much weaker.
H. Weaker claws, cannot hold on so well.	Strongly developed claws and toe-musculature.

[Image 20] (Cullen, 1957:298–300)

Cullen's work showed a new direction to the Tinbergians. It built on a modified form of the ethogram because in order to make her comparison here she first had to observe and compile the list of behaviours that were characteristic of this species. After doing this she was in a position to compare them to the ground nesting gulls studied by previous Tinbergians including Moynihan and Tinbergen himself. Cullen shifted what it was possible to include in an ethogram to accommodate also a range of not so strictly behavioural considerations. For example the observations on the nest include considerations of the nest–building process, the places that material are gathered, the physical structure of the nest itself, and the observation that the nest is 'guarded'. Observations of the physical structure of the nest are certainly important for drawing out her comparison with the ground–nesting gulls, but they are also not the standard fare of Tinbergian observation.

Other aspects of Cullen's work helped to further this picture of total adaptation of all aspects of a species biology, including its behaviour.[139] Cullen and later Tinbergen were both conscious of this shift to incorporate evolutionary investigations which included behavioural modifications, and morphological changes to better suit a species' environment. For example under this theoretical framework, the shift to a lessened alarm call[140] that Cullen notes is a behavioural consequence of cliff nesting

139Burkhardt calls this view 'a comprehensive adaptive system' (Burkhardt, 2005:418), but I have not traced the phrase in Tinbergen's own writing. Nevertheless, I feel it is a very clear rendering of the idea that Tinbergen and Cullen were describing.

140I can only presume that in identifying a 'lessened alarm call' for an ornithological audience, Cullen could rely on them to understand whether this meant less noisy, shorter or involving less

because predation has been lessened due to the physical difficulty of getting to the nests; likewise Cullen also points to the 'strongly developed claws and toe musculature' (Cullen, 1957: 300), which is a morphological consequence of the same evolutionary and adaptive process. Tinbergen began to frame his work and ideas in a way that reflects an interest in Cullen's ideas by 1959 (Burkhardt, 2005:418), but even a year earlier Tinbergen had described Cullen's work as giving great insight and showing how evolution works on all aspects of a species: 'Seen from this angle, the Kittiwake stands as a beautiful example of the general rule that adaptation involves the whole animal' (Tinbergen, 1958: 204). By using the term 'whole animal' Tinbergen is showing that not only does evolution act on morphology but also behaviour, and furthermore that both of these areas are properties of a 'whole animal'. Cullen's work was then genuinely a transformation point, as it combined the early ethological approaches – the focus on observation and the compiling of an ethogram – with what would be the characteristic of the later school, the emphasis on systems and adaptation and evolution.

Cullen's work not only marked a shift toward an adaptationist perspective, but also heralded a more interventionist and experimental approach to fieldwork. This shift in methodology was certainly neither instant, nor without precedent, the red spot tests on gulls. Tinbergen's mentioned in the introduction, were performed under field experimental conditions. However these were built on his work in the Netherlands, and this did not appear to be a practice that carried over regularly into the early field school in Britain. Tinbergen's fieldnotes record a handful of chicks that were brought in for study, but his recording of what was done to them is patchy, and these observations were not the basis for any scientific papers. Had they not been mentioned in Curious Naturalists (1958) it would have been possible to miss them entirely as they only take up a few lines in the many volumes of fieldnotes.[141] By contrast in the Netherlands he had regular contact with chicks, initially attempting to

extraneous movements, as this is not specifically outlined in her paper.

141 The only mention of the bringing of the birds inside in Tinbergen's fieldnotes is as follows:

> June 17 1951
> Later on day we find one gull chick just hatched (a little wet) we take it home, keep it in cardboard box on corner of stove and take number of tests with it,
> In the afternoon we leave it at home, which chick keeps calling distress call until we cover it with a lid of a sugar bowl, means that cover by handkerchief or even tea cloth was not enough but it must be somewhat heavier. (Tinbergen, 1951, MS.Eng.e.2749)

research them in the nests, but later bringing them into tents as the nest research proved impractical.

> At first we presented the chicks with our dummies while they were in the nest. This gave us some responses, but only very few, for the chicks crouched, presumably as a consequence of the alarm calls of the adult birds, which were flying around our heads all the time. We decided to carry the chicks to a quiet spot outside the colony. To be sure that passing gulls would not give the alarm–note and thus disturb our work, we put up a tent, and made ourselves and the chicks comfortable in it. (Tinbergen, 1953: 198)[142]

Cullen's work fits with this more experimental and interventionist approach when she was investigating chick behaviour, rather than the purely observational approach. This work involved both chicks and eggs from a variety of different species, (chiefly herring gulls blackheaded gulls and kittiwakes). She put the eggs of ground–nesting herring gulls and blackheaded gulls into kittiwake nests to see if the fact that kittiwake chicks do not move or run in response to predators (as they live on cliffs and predators are extremely rare) was innate. This is her account of what she observed:

> On the other hand two young Herring Gulls and one Black–headed Gull which were hatched and reared in Kittiwakes' cliff–nests would all have run over the edge of the nest had I not prevented them by fastening wire–netting round the nest–rim. From this and Salomonsen's observations[143] we can conclude that the difference in running between the young of the different species must be innate. (Cullen, 1957:289)

This report is interesting for the amount of intervention that had gone on to perform this experiment: setting up wire–netting, obtaining eggs of different species and

142Tinbergen is here revealing his earlier Dutch work to the later British audience, hence the date may appear somewhat anomalous to the astute reader.

143Cullen is referring here to the work of the Danish ornithologist F. Salomonsen, 1941 'Tretaaet Maage (*Rissa tridactyla* (L.)) som Ynglefugi I Danmark.

switching them, as well as recording the resultant behaviour. Though we might perhaps question whether the wire netting was really used since, had there been wire netting around all of the nests, there would be no way of telling whether the chicks would imperil themselves in its absences. In fact, Tinbergen gives a rather different account of the same situation:

> It was naturally interesting to know whether this difference between young Kittiwakes and other gulls was innate or perhaps imposed upon them by the different environment in which they found themselves. To find this out, the Cullens put some eggs of Black–headed Gulls and Herring Gulls in Kittiwakes' nests. They were accepted and duly hatched, but most of the chicks did not survive very long, for, showing not the slightest inhibitions, they soon began to walk about with disastrous consequences. The converse test, having been published about a small Kittiwake colony on a Danish island, where, for unknown reason, Kittiwakes nest on flat ground. Salomonsen, who has visited this colony comments on the fact that even here the chicks stay in the nest, under circumstances where chicks of other gulls would move about. There is, therefore, no doubt that we have to do with a real, innate difference between Kittiwakes and other gulls. (Tinbergen, 1958: 203)

Cullen's work clearly showed the innate nature of the behaviour differences between habitually cliff–nesting Kittiwakes and their habitually ground–nesting gull cousins. However in order to uncover this she used quite different methods to her field predecessors. The relationship between the observer and the observed is quite different in Cullen's observations from those of Moynihan. Where Moynihan's work was largely observational, Cullen's observations were made under much more interventionist conditions, not least because there was direct switching of eggs, and also perhaps considerable nest–environmental changes with the alleged application of wire netting around it.[144] This was definite a sign of the drift toward intervening in

144Hide had intervened in the lives of his birds by placing automatic recorders in their nests, but the intervention was very different as this was in order to monitor natural behaviour, rather than learn by experimentally changing variables as Cullen did.

the field, and this was a trend that would continue.

The change to greater intervention in the field is apparent in much of the later work of the school, as is the shift toward a focus on adaptation. In the early years of the school, the interests had been on stimulus and response, as in the red–spot tests, and on generating ethograms, as Moynihan's and Morris's work had attempted to do. There was genuine enthusiasm in the school about Cullen's type of work (Tinbergen 1958:268) particularly in its focus on adaptation and use of interventionist field experiments. Cullen had herself done extensive further experiments with eggs, in which she exchanged further species' chicks, adding to the herring gull and kittiwake also the shag, in experiments to ascertain whether kittiwake parents could recognise their own young (Cullen, 1957: 296–7). The result was quite clearly that they did not, especially as kittiwakes and shags are completely different in appearance – shag chicks are entirely black with long beaks, and kittiwakes' chicks are largely light grey, with much shorter beaks. To Cullen's ornithological audience[145] the difference would have been apparent immediately, and so the failure of kittiwakes to differentiate their own young would be correspondingly interesting. Her work, tailored to this ornithological audience rather than evolutionary theorists, helped to point towards the study of adaptation as the central research object of the school. Her innovative use of eggs rather than chicks was also continued by others in the school after she had completed her research, as we shall see next.

Section 1.2 Colin Beer's egg work

Egg work with an adaptationist approach was carried to the later research locations of the Tinbergians, particularly the new camp at Ravenglass in Cumbria.[146]

145Cullen's work was published in Ibis, the journal of the British Ornithologists Union, which had a wide, readership amongst professional and leading amateur ornithologists but was not solely a behaviour journal.

146The earliest work of the British Tinbergians was at Scolt Head Island off the Norfolk Broads, now a national nature reserve. Later, the Cullens worked on the Farne Islands off Northumbria, where kittiwakes were in abundance and where arctic terns were also found. This rotation of research site was a deliberate policy of Tinbergen's (Tinbergen to Burkhardt, 1976, MS.Eng.c.3125 A.4) as he tried to rotate the site every 10 years, though he gives little explanation for this except to suggest that it helped with 'variety' and in presenting 'new challenges'. As far as the Farne Islands, Cullen's research site, was concerned Kruuk has the rather heart–warming observation that Esther Sager (as she was when she arrived in Oxford) and Mike Cullen were sent there by Tinbergen with not

Ravenglass had a very large blackheaded gull colony living on large area of sand dunes on the Cumbria (at that time the county was called Cumberland) coast.

One student whose work clearly followed Cullen's interest in egg studies was Colin Beer who worked at Ravenglass on egg–rolling in the blackheaded gull. His work represents another transition point in the way that the school was evolving, and it is his method that interests me especially. Building on the approaches of Cullen, and particularly on Cullen's contemporary Rita Weidmann,[147] on egg–swapping and egg-rolling respectively, Beer also chose to intervene in the gulls' lives in order to understand their behaviour of egg retrieval. This behaviour, which consists of rolling eggs that are outside the nest, into the nest was thought to be functional (that is of significance for the likely survival of the species). Beer followed the reasoning that if it were to be functionally significant then it should be more easily stimulated the nearer they got to egg–laying season, as he assumed that this would be when the action of putting eggs in the nest would have a survival value; during the remainder of the year it would have no value, and so the response to an egg outside the nest would be less likely to be activated (Beer, 1960:373–374). It is Beer's methods however that interest me most as they show how much the switch away from pure observation and toward greater intervention had occurred.

Importantly, Beer's work involved a change to large scale survey work, with a relatively small proportion of time spent on direct observation:

> I used two techniques. First a rough method which could be carried out on a large scale:– In the mornings I placed wooden egg–models (normal shape and colour) outside a number of labelled nests – the models were placed 9 inches from the nest centre and the ground or sand smoothed to facilitate successful rolling. I collected the models 6 hours later and recorded how many were inside the nests. Daily visits to the nests

entirely scientific aims. “Niko put Mike and Esther on the Farne Islands for their fieldwork, with a twinkle in his eye, and Esther Sager became Esther Cullen.” (Kruuk, 2003: 167).

147 Rita Weidmann née White studied blackheaded gulls particularly looking at their food begging responses, and therefore looking for equivalent responses for food–begging and pecking that were got with herring gulls and their chicks over the red–spot tests. See Weidmann, (1956).

> established when, in relation to laying and hatching dates, a particular test was made...
>
> The second method I employed was to set up the same standard situation as in the rough test and watch the nest for 2 hours. There was time for only a relatively small number of these watched tests but they gave me some idea of the reliability of the trends shown by the rough method. Further, they gave me two more measures of rolling tendency – the latency between arrival of the test birds and their response; the number of rolling attempts made. (Beer, 1960:374, 376)

Beer's second method here shows the definite imprint of what had gone before, emulating for instance Moynihan's ability to watch the nests for 2 straight hours; but this is very much secondary to the results gained from more interventionist approaches – namely placing fake eggs next to nests. The main body of Beer's research follows the approach pioneered by Cullen, with intervention followed by later recording. Beer's egg–swapping experiments were based on similar methods to those of Cullen's – based upon placing items into nests and observing and monitoring the behavioural consequences, though where she had placed eggs of different species into nest Beer placed fake eggs. Beer's results showed quite unambiguously that the nearer one was to breeding season the more likely one was to elicit egg–rolling behaviours in the birds by placing fake eggs by the nest:

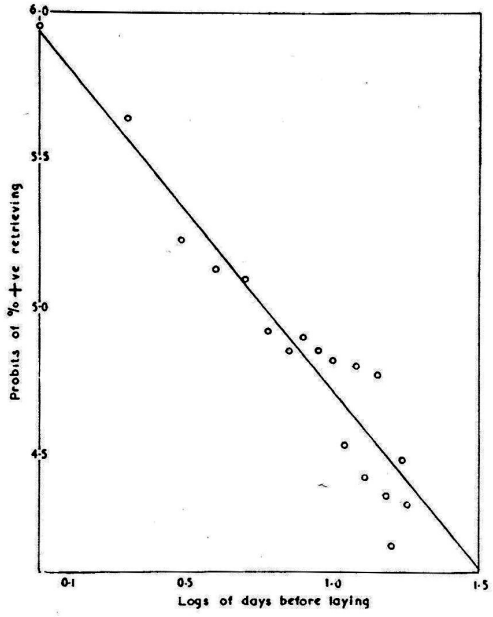


FIG. 13. Pre-laying period egg-rolling. Figures transformed and plotted to show how percentage of eggs rolled increased as the date of laying drew closer. See text.

[Image 21] (Beer, 1960:377b)

Theoretically this is a nuanced step on from the early ideas of behavioural units released like locks with keys. Now the approach has changed towards a system of understanding based upon likelihoods of eliciting a certain response. That is an ontological shift, even if it is not one commented on directly by the Tinbergians. It is one thing to talk about an absolute mechanism which is activated or not by a single stimulus under all circumstances, as was claimed in the literature on the Lorenz–influenced Innate Releasing Mechanism. It is quite another to say that environmental circumstances govern the likelihood of that mechanism being switched on. Here the nuance emerges from the greater focus on survival value, where Beer saw that the behaviour was more likely to be released when it was nearer to the breeding season, and argued that this was because it was of greater survival value then. From an evolutionary perspective there is no rationale to develop a behaviour of rolling eggs into the nest until it is likely that they are your eggs, and therefore the behaviour should become more likely to be performed the nearer the birds are to egg–laying.

Section 1.3 Kruuk and Tinbergen's egg–shell work

Beer's work was the first of a whole set of field studies on this type of problem, analysing the survival values of specific behaviours, using more interventionist experimentation, and generating more mathematically sophisticated analyses of their observations. These studies all emerged from Ravenglass, the Tinbergians last major research site in Britain, and it is here that Tinbergen along with a large number of students carried out studies on the phenomenon of egg–shell removal and its potential survival value. At the same time that Beer was finishing his research Hans Kruuk joined the Tinbergians, so it is worthwhile for a moment considering his account of these experiments:

> During those first years in Ravenglass Niko once more began to feel the need for his own field research project, something that he had missed out on for more than 10 years. Here he had the opportunity to start one, and there was an ample supply of volunteers to help. Colin Beer's observations[148] provided the last push, and Niko started to experiment with gulls and eggshells. The gulls' eggshell removal was a particularly fortunate find, because Niko could investigate combined questions: what made gulls do it (similar to the model experiments he had done in his earlier career), and what was the function or survival value – what are the benefits that the birds gain from it? Function of behaviour had become a major interest to him, and there was something in this particular case that was especially attractive: the very insignificance of the behaviour, an action that did not occupy the birds for more than a few seconds every year, and which was of doubtful importance.[149]

148Beer had studied the nest–building and incubation behaviour of blackheaded gulls from extremely close up: '

> One of Colin's activities involved watching incubating gulls from underneath, with Colin in a coffin–shaped, buried, observation hide lying underneath a sitting bird that he had enticed to nest on a horizontal glass window. This study of the behaviour patterns affecting egg–laying and incubation was clearly on the boundary between ecology and ethology, one of the beginnings of behavioural ecology.' (Kruuk, 2003:210)

149Kruuk does not explain why Tinbergen's interest had shifted toward questions of adaptation, and I can see nothing from his letters that directly explains it either. Tinbergen does mention his interest in adaptation in a letter to W.H. Thorpe, (Tinbergen to Thorpe, 8th September 1976, Tinbergen Archive, Oxford, MS.Eng.c.3125 A.4), however this letter, which I will examine in more detail below suggests that he was influenced in his study of adaptation by urging from Konrad Lorenz

> The eggshell–carrying study began in 1959. It was very much Niko's project, lasting three years. Every year there were three volunteers to do the donkey work, with Niko himself taking part whenever he was around. The volunteers were mostly non–Brits, post–docs from South Africa, Poland and Switzerland, students from Holland who were doing work for their MSc– equivalent degree, or from France, and there was a teacher doing a sabbatical. I was one of the Dutch helpers, arriving in the second year of the project. All of us worked alongside the PhD students who were doing their own projects. We discussed in great detail questions such as whether eggshells could endanger the brood by attracting predators, and how one could test this. First we had to show that the egg's camouflage colour was effective, so out we went with black–headed gulls' eggs. We put them out in the dunes as well as gulls' eggs painted white, and yes, the white eggs were taken in no time by the crows and herring gulls, and many of the natural eggs were left alone. Only then could we check whether the presence of eggshells would endanger a gulls egg, in a similar experiment, and yes it did: more of the eggs with eggshells next to them were found first. We did scores of such trials, and in the colony we presented dummies on nests, eggshells, rings, squares and half ping–pong balls of any colour, and scored the percentage removed by the gulls after half an hour.
>
> The enthusiasm in these early–morning sessions of the field–experiments was enormous. We watched the predators and our experimental set–up, and if we came back to the caravan with another 'good' result and lovely observations there would be cheers from the boss. If things went the 'wrong' way, that is if results were unexpected, Niko would find it 'interesting', and we would think it maddening... (Kruuk, 2003, 211)

Kruuk gives us a real sense of life in the later field school with the constant experiments and interventions in the life of the gulls under study, which are detailed

and Jan Verwey.

in the great team paper of 1962(Tinbergen et al, 1962).[150] He also gives a sense of how much the school's focus had shifted from the pure stimulus–response work of the early era and into work which incorporated stimulation in a framework of adaptive evolution. It is significant that he chooses to flag up Tinbergen's growing interest in questions of function and survival value as something that they themselves recognised at the time. This is the later school at work, with its interest in survival value and adaptation, features of the study of animal behaviour which would outlive the science of ethology. In the paper itself, the writers credit the Cullens' studies as being crucial in their understanding of behaviour, describing their influence as 'stimulating' (Tinbergen et al, 1962:111). The possibilities of doing integrated studies, combining stimuli–response work with evolutionary approaches, had been so wonderfully shown in Cullen's exemplary work (in both the Kuhnian and lay sense of the word). Beer's work had also shown that such a combination was possible, and pointed to a more subtle understanding of the releasing mechanisms themselves. The work of the later Ravenglass group was more theoretically complex still, as they began to discuss the interplay between different selective mechanisms, and the idea of different selective pressures, which was a significant switch in the evolutionary understanding of behaviour. Cullen had focused her work on how a single change in the habitat of a gull species, from nesting on the ground to nesting on cliffs, had produced significant adaptations both morphological and behavioural. By contrast the later Tinbergians began to study how in addition to the problematics raised by Cullen, different evolutionary solutions could also interact and cause complex compromises in the behavioural adaptations of a species. This both built on, and also altered the way that work on adaptation was being done by the Tinbergians. It was quite a step on from Cullen's work with its neat single change causing many further ones, into a world of partially competing and partially complementary systems that all influence the responses to a broken egg shell in the nest:

150This included an extraordinary number of researchers for a Tinbergian paper. Esther Cullen published her first work on her own, for example, as did Desmond Morris and Martin Moynihan, and others like Margaret Bastock published with only one or two colleagues. This 1962 paper credits: N. Tinbergen, G. J. Broekhuysen, F. Feekes, J. C. W. Houghton, H. Kruuk, and E. Szulc. Other than Tinbergen who was at Oxford, the other writers were attached to respectively: University of Cape Town; University of Utrecht; City of Leeds Training College (now a part of Leeds Metropolitan University); University of Utrecht again; and the Nencki Institute of Biology, Warsaw.

> On the whole, the gulls' response is very well adapted to its main function of selectively removing the empty shell, but the relatively high scores for objects which have very little resemblance to egg shells suggest that it is adapted to the removal of any object which might make the brood more conspicuous.
>
> A pilot test showed that gulls which have incubated black eggs respond better to black egg shell dummies than normal gulls.
>
> The lack of promptness of the response as compared with non–colonial [151] waders (Ringed Plover and Oystercatcher) is adaptive, since it tends to reduce predation by other Black–headed Gulls, which are shown to prey selectively on wet chicks. A hitherto unrecognised function of territory is suggested.
>
> In a discussion of the entire anti–predator system of the Black–headed Gull its complexity and its compromise character are stressed: the safety demands of the individual clash with those of the brood; there are conflicts between the several safety devices which each benefit the brood; and there are clashes between the ideal safety measures required by each type of predator. (Tinbergen et al. 1962:115)

This paper, which Kruuk calls 'one of the Tinbergen classics' (Kruuk, 2003: 213) neatly brought together the new approaches of the Tinbergians in the field in the 1960s. Kruuk suggests it was a turning point for Tinbergen personally:

> One important consequence of the eggshell study was that it gave Niko the confidence he needed for more research on the biological function of behaviour, on what behaviour is for, on its survival value. He had now demonstrated that one can do proper experiments on such questions. From this time onwards, the focus was on function, for himself and for his students, and work on causal aspects of behaviour, so very important in Niko's group until then, was sidelined. (Kruuk, 2003: 213).

151Non–colonial meaning in this instance not nesting in large colonies.

This later interest in survival value ranged over both the fieldwork, and also ,as we will see in the next section, the laboratory work. It gave the group a real impetus in their research, as the early post–war phase had. Instead of merely looking for localised statements about the stimulation of behaviour they could be observing evolution in process in nature.[152] This new approach of trying to experimentally disentangle selection pressures captured Tinbergen's own imagination as much as it did that of his students, and it provided him with a body of work with which he could engage in the vigorous wider debates of the period. He felt very strongly that it was a major advance to be studying survival value experimentally in nature and that because of this he could criticise other ornithologist biologists who were interested in selection, as he explained to Ernst Mayr in a letter from 1968:

> Some day we ought to talk about the kind of thing that I once more tried to explain in my IOC contribution – groggy as I then was: my hobby horse of identifying selection pressure, and the way they do their pressing, by means of our studies of "survival value". Somehow I feel that you are not very much interested in this, and yet I feel that you ought to! Admittedly this kind of work has fairly modest aims; yet I feel a contradiction in your saying "the environment is the important agent" and your (seemingly???) lukewarm attitude to our attempts to check up with experimental methods – <u>in</u> the environment. (Tinbergen to Mayr, 9th January 1968; HUG(FP) 14.17)

Tinbergen's concern to study evolution in the natural world was profound, and he believed that study there would reveal answers not available to laboratory workers: 'our field analyses reveal time and again the most unexpected pressures' (Tinbergen to Mayr, 9th January 1968; HUG(FP) 14.17). These unexpected results were the best justification possible for the field study of evolution, as they were based on

152Burkhardt suggests that it was important for Tinbergen that fieldwork could be shown to contribute to evolutionary debates: 'fieldwork was the key to unlocking special insights about behavioural evolution. Fieldwork made it clear that the displays of the kittiwake are not arbitrary conventions but instead are ultimately related to the species' cliff–dwelling habit.' (Burkhardt, 2005: 420). Burkhardt argues that for Tinbergen, Cullen's work showed the value of field observation as a research approach: 'Field observers, he maintained, were in a position to discover things that observers of animals in captivity were not.' (Burkhardt, 2005: 419)

observations not available to traditional laboratory workers. Tinbergen's great methodological opponents, the Behaviorists, would never have had the chance to understand the complex behaviours he was able both to identify, and with this survival value framework, explain. Even his own laboratory students would have had difficulties in identifying these different possible selection pressures, because having extracted the animals from their natural environments, they would not be able to see the various and conflicting selection pressures working on them. The egg–shell studies provided Tinbergen with the perfect demonstration that fieldwork was indispensable for understanding evolution and adaptation. However because his work was a study of the behaviour 'egg–shell removal' he could demonstrate that *behaviour* was an irreducible part of the evolutionary process, and therefore that the field study of behaviour had significant contributions to make for the study of evolution and adaptation.

Section 1.4 Blurton–Jones returns to old territory

Nick Blurton–Jones was one of Tinbergen's later students whose work blended a range of the traditions and tendencies of the earlier school, though creating a mixture quite different to that of McLannahan above. Blurton–Jones focussed on the great tit, the same species studied by Robert Hinde in the early school, even working at Wytham woods the same research site. However Blurton–Jones applied the methods that had emerged over the intervening nearly twenty years to the study of this animal. Blurton–Jones set out to build experiments upon observations, as a good Tinbergian should, but he clearly believed the observations of Hinde and the others in the earlier period had led to not much more than circumstantial levels of knowledge on the subject:

> The main aim of this study was to test the theory outlined by Tinbergen (1952 & 1959)[153] that "threat" displays are a result of simultaneous elicitation of the behaviour patterns of attack and fleeing. I studied such displays in the Great Tit (Parus major L.) whose behaviour

153All of the literature referenced here is in my bibliography.

> had been extensively studied by Hinde (1952).[154] He described most of the displays and produced evidence that their causation was indeed a conflict of tendencies to attack and flee.
>
> Most of the evidence for this theory is circumstantial and I aimed at eventually carrying out experiments which would test it directly. But first I used interpretative, non–experimental methods usually applied in such studies in order to derive hypotheses about the causation of the displays and compare these hypotheses with those found in the literature. Then I went on to the experiments, working deductively, trying to create the conditions thought to be necessary for the appearance of the various displays and checking whether the displays actually occurred. This, besides checking my hypotheses about Great Tit displays and the general theory of conflict causation of threat displays, provides a merely empirical check on the validity of the methods used. (Blurton–Jones, 1964:1)

Blurton–Jones then, has shown another way that the Tinbergians changed over time in the field. His work begins in conventional style with the observation of wild behaviour in nature, but subsequently moves in a highly experimental direction, in order to test Tinbergen's theories about “threat displays”. Blurton–Jones asserts above that until his work had been undertaken, the evidence for these previous theories was at best 'circumstantial'. He still chose to run through the formality of a long period of standard pure observation, even though he suggests that acknowledges displays of the great tit had been extensively studied in Hinde's earlier work. This shows a continuation of the methods of pure observation for which the school was so famous, but it also shows how observations were no longer treated as generating sufficient evidence in themselves, and by this point were augmented as standard by evidence from experimentation.

Blurton–Jones's experiments were conducted entirely in the field, and were sited near to either wild–positioned nest boxes or bird tables. In the example below, he tested

154This refers to Hinde's *Behaviour Supplement,* published as: 'The Behaviour of the Great Tit, *Parus Major* and some related species', *Behaviour Supplement,* (1952).

the strength of the motivation to feed or to flee by offering food and comparing the responses when, for example other (stuffed or live) great tits were present, or when (stuffed) predators were present:

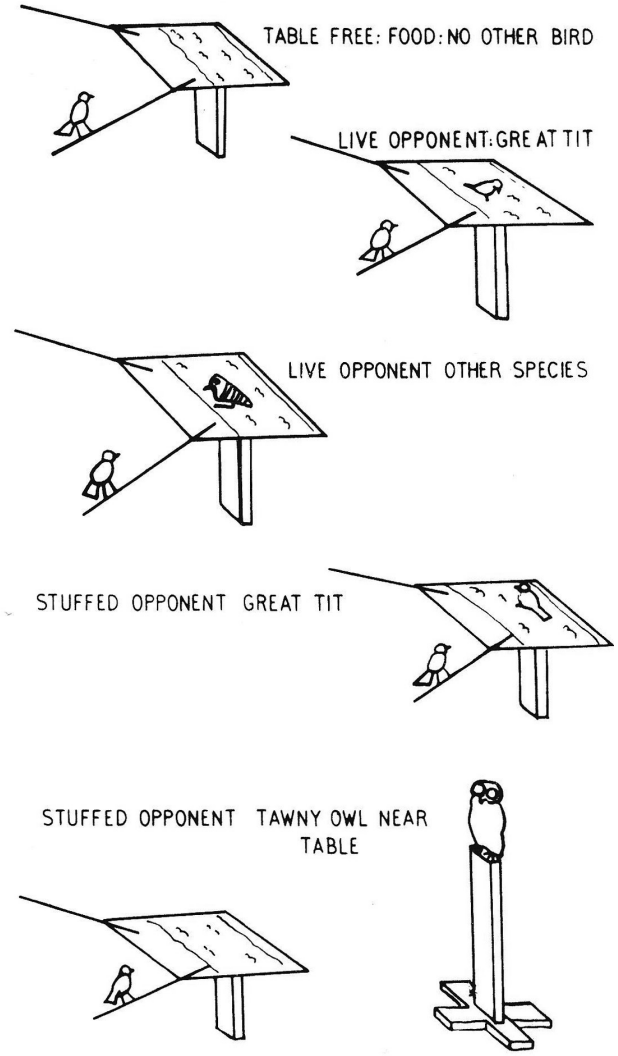


Figure 2. The various situations at the bird table.

[Image 21] (Blurton–Jones, 1962: 11b)

Parus major (the great tit) is here studied by altering the environment that the wild birds would otherwise be existing in. There is the presence of the bird table itself, along with the observation hut (not shown). But once the tits have become accustomed to these presences (a shift from the focus on purely innate behaviour of

the early school) other models are introduced in order to study their responses to them. This recalls the experiments of Morris in his fish tank, using a large range of models in order to see which generated the greatest and the least responses and thereby understand what stimulated specific behavioural responses. Blurton–Jones's work however involved studying the birds' responses to a range of different stimuli, which were intended to represent the responses of the tits to a range of different birds, including potential predators. Predators were certainly not a part of the earlier studies by either Hinde in the field or Morris in the laboratory. What the introduction of predators as a stimulus represents is a transition toward survival value becoming a principal object of study in the school. Blurton–Jones was taking the new approach suggested by Cullen's Farne Island work, and developed in the egg–shell work at Ravenglass, and applying it to Hinde's old bird, at Hinde's old research site. The complexity that was beginning to be developed at Ravenglass was also in evidence here, with Blurton–Jones noting that the stuffed owl released many similar behaviours to those observed in response to live predators (Blurton–Jones 1964:16). Blurton–Jones however linked this to the immediate stimulus and responses that he was observing, thus showing that stimulatory questions and answers which had been open to Moynihan's generation of ethologists were still present, but also showing the influence of the new post–Cullen evolutionary approaches:

> If a Sparrow Hawk flew by or an alarm call was given nearby, and sometimes if a person came suddenly into the clearing, the birds on the table would fly very fast downwards into the undergrowth. This “Diving” would obviously be adaptive as a response to Hawks. (Blurton–Jones, 1964:16)

This quote is particularly illuminating because it contains features that would be similar to the Moynihan era work, specifically the labelling of the behaviour “Diving” with a non–functional word, akin to Moynihan's “Choking”.[155] However

155Another comparison could be made to Hinde's work, though Hinde was subject to more influences which makes the picture more complex. Nevertheless his work does mention great tits responses to predators, but only from a stimulus–response point of view, and without the adaptationist framework for understanding:

> Tits show two responses to avian predators. If the predator is in flight, they take cover in think bushes and utter a special alarm note. If the predator is perched, they come towards

whereas Moynihan's work aimed at describing the behaviour in as much detail as possible, and bracketed off the explanation in anything more than context derived terms, Blurton–Jones sees the explanation in evolutionary and adaptational terms. To compare the two we could perhaps imagine Moynihan watching the same behaviour, and drawing attention to the hawks as the stimulus for it, but certainly not going further than that. To Blurton–Jones however the adaptationist framework is so secure, that the functional significance of the behaviour is clear; it is 'obviously adaptive'.

Section 1.5 Heather McLannahan and the return to chick studies

McLannahan's work, which began after Blurton–Jones's had finished,[156] followed on in both theme and methodology from Esther Cullen's work on kittiwake chicks, though in a more humane way. Where Cullen had studied the innate responses of kittiwake chicks through the egg–swap experiments with their associated collateral damage, McLannahan set up artificial cliffs in the field and even went as far as setting up incubators for the eggs and then (still in the field) testing the chicks on a range of different surfaces to ascertain what factors made them move or stay still. She found that kittiwake chicks were inclined to crawl up slopes, also and more strikingly that even very young chicks would not cross a visual precipice. McLannahan, (shown below undertaking the field experiment) demonstrated that there was a two part response that had evolved to keep the chicks safe, involving both visual and touch stimuli. Tinbergen described in detail the nature of the experiments performed by McLannahan:

---

it and scold it in a manner similar to that used against human intruders in spring. (Hinde, 1951:x)

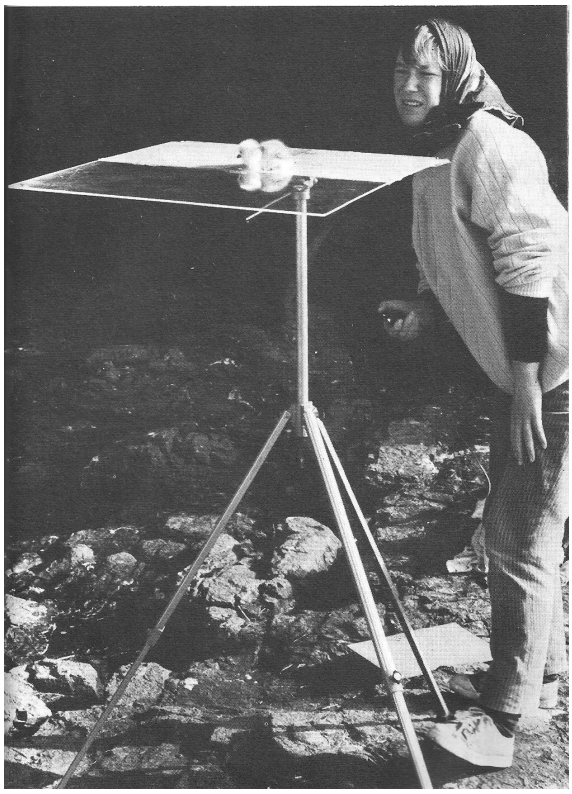
This paragraph, which monitors similar behaviours, has, however, no adaptationist framework in it. It was enough to record the behaviour, and describe what stimulated it. This again illustrates the change there was between the early era and the work of the later period of which Blurton–Jones's was a part.

156Blurton–Jones began his work in 1959 and his D.Phil. was accepted in 1964. Heather McLannahan began hers in 1967 and completed it in1970.

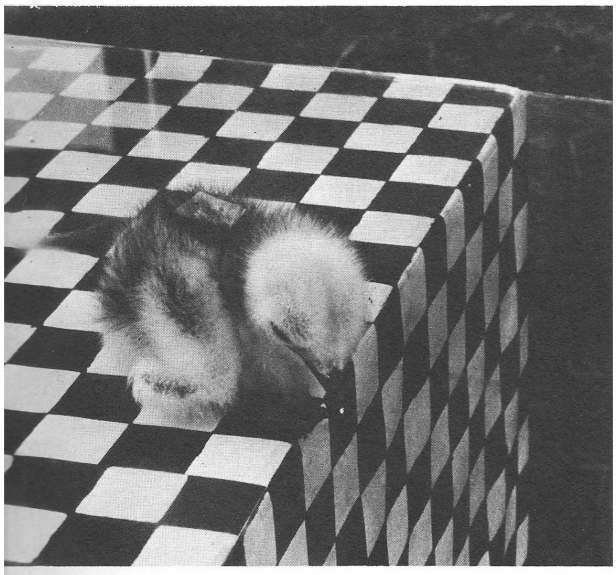
> First, she decided to take eggs from a kittiwake cliff and hatch them in little boxes inside an incubator, to make sure that the chicks could never have seen a cliff before they came to be tested. In addition, anticipating that she would see efficient edge–avoiding responses, she decided to test straight away by what sense organs such a response would be controlled. It was likely that they would use their eyes for this, but they might also be able to feel the cliff's edge – a response that would stand them in good stead during dark nights. To test the effect of visual stimuli only, she used what is commonly called a 'visual cliff'. This consisted of a transparent glass or perspex plate, of which half was lying immediately on a visibly solid structure, while the other half extended over a yawning abyss, which could be seen but, because of the perspex plate could not be felt. The top, the vertical face and the bottom of the 'cliff' were painted in a chessboard pattern of white and black squares, each measuring 2x2 centimetres. This made the whole situation clearly visible to the chick, and also allowed Heather to measure the extent of its movements.
>
> For a test, a chick was taken from an incubator with its head carefully screened and was placed exactly on the edge of the 'cliff' – in some tests with the head just above the 'abyss', in others with the head above the 'ledge'. The chick was then allowed to see, and its behaviour was carefully watched. The results were very striking indeed, particularly in the first type of test. The chick would look round and would soon see the abyss, and then it would at once crouch, tremble all over its body, even spread its tiny wings, and try to hook its claws into the substrate. And at the same time it turned and crawled away from the 'edge'. A couple of centimetres or so from the 'edge' it would relax, the trembling would stop, it might even stand up and preen itself – all signs of being at ease once more. (Tinbergen, 1974: 249)

As well as writing about this, Tinbergen also took a series of photographs of these field experiments, some of which cans still be found in his archive. On the next page there is one showing McLannahan at work herself, and a close-up image of one of

the kittiwake chicks on the apparatus itself.



[Image 22](From Tinbergen, 1974: 249)



One of the chessboard tests: a kittiwake chick about to turn away from the visual abyss.

[Image 23] (Tinbergen, 1974: 250)

This is very far from the type of early fieldwork that Martin Moynihan was doing, and even quite a few steps on from Cullen's own work. In its title McLannahan's publication – 'Some aspects of the ontogeny of cliff–nesting behaviour in the Kittiwake *Rissa tidactyla* and the Herring Gull *Larus argentatus'* (1973) – very strongly recalls Moynihan's work, which had been titled: 'Some aspects of the reproductive behaviour of the Black–headed gull and related species.' That the substance of McLannahan's work is very different to Moynihan's, with no interest in ethogram generation.

McLannahan's work uses considerable intervention in the lives of the chicks studied. The kittiwake chicks were raised from eggs, hatched away from their parents, and were tested on perspex sheets for their innate responses to visual cliffs. Esther Cullen had previously observed that kittiwake chicks tended to be entirely sedentary, an observation made as part of studying their whole adaptive system, which in turn had

followed a partial listing of a range of behaviours (the ethogram). McLannahan, by contrast, had looked only at a very small part of the behaviour of the kittiwake, namely the chick's responses to cliffs, and by the content of the study it is evident that she was specifically working to better understand the earlier observations made originally by Cullen. Indeed McLannahan's study only makes sense as a continuation and focussing of Cullen's.

The practical methods show a considerable change, moving from Cullen's rather rough–and–ready approach, using only the eggs and the pre–existing nests of the birds themselves, to McLannahan's much more prepared approach, using eggs hatched in incubators, ready painted boards, perspex sheets, and stands, as was shown above. In doing this McLannahan's work reflects the creeping interventionism of the field experimentation by the late period of the school. Her work also shows the growing overlap in method and approach between the field and her laboratory colleagues, whose work we will discuss in the next section. McLannahan, like Tinbergen and Kruuk whose work on egg–shell removal I outlined above, shows how much the field school changed over the period of Tinbergen's time at Oxford. They show transitions in methods and in theoretical object, with the field school becoming more experimental in approach and more interventionist in the lives of the animals they were studying. They were also concerned with understanding behaviour in evolutionary context rather than solely looking for answers to stimulus and response questions as Moynihan and other early workers had done. Cullen's paper, which is now seen as a 'classic' (c.f. Danchin and Nelson, 1991), was a real turning point in this, showing how a set of mild interventions in the lives of the animals could help in understanding quite large questions about their evolution and behaviour. This focus on understanding behavioural adaptations is also evident in both the work of Tinbergen and Kruuk on egg–shell removal, and in McLannahan's interest in unravelling the complex behavioural responses of the kittiwake chicks she was studying in order to better understand the individual adaptation under study.

Blurton–Jones and McLannahan were amongst the last students that Tinbergen supervised in the field. They also represent the culmination of the processes acting on

the fieldworkers, though in subtly different ways. McLannahan's work with its highly experimental approach is profoundly different to the early observational studies of Moynihan and others. Instead, following Esther Cullen, but going much further in the same direction, McLannahan was prepared to intervene in the lives of her birds directly by moving their eggs into hatcheries, and by placing the newly hatched chicks onto artificial experimental surfaces. Theoretically also McLannahan's work shows how much the school had shifted, as it had no interest in ethograms (unlike Cullen) and focussed only on small questions on one aspect of the kittiwakes' adaptation. Blurton–Jones is different because his work was certainly more experimental than the previous Tinbergian to study great tits: Robert Hinde. He intervened quite severely in the lives of the animals he studied, but his work shows that the two seemingly distinct eras of Tinbergian study in the field, the early and later periods, were far from divorced from each other. Instead he took stimulus and response observations and combined them with the new adaptationist framework emanating from Ravenglass. McLannahan's work represents a similar process of change–with–continuities, taking up studies on Esther Cullen's favoured kittiwake chicks, but extracting them from their natural environment and placing them in a purely artificial experimental context. Nevertheless both Blurton–Jones and McLannahan were still interested in understanding the natural or innate behaviour of the species they were studying – their interventions were designed always to elucidate innate capacities rather than, for example, learned behaviour. In this latter sense their work, though with a much more explicitly evolutionary outlook, still sought to understand the same objects as that of the very earliest Tinbergians.

Section 2: Watching Nature in the later laboratory

The later Tinbergian laboratory was significantly different to the place that had been inhabited by Desmond Morris and Margaret Bastock at the start of Tinbergen's time in Oxford. There was further cross–over with the fieldwork, with new field–derived methods, theories and techniques that I discussed above arriving in the laboratory. The laboratories themselves changed physically, incorporating substantial new

aviaries to monitor bird behaviour. There was also change in the animals the laboratories contained, for example adding new species of birds, including the domestic chick. There was also a shift in interest with neurophysiological questions studied by means of brain–stem stimulation, a far cry indeed from the early observational and non–interventionist ethos of the school.

This section will examine three people's work and relate it to the general trends of the later school. Specifically I will be looking at three of Tinbergen's students and their work – firstly the later work of Desmond Morris, secondly Richard Dawkins's studies of chick pecking, and thirdly Juan Delius's work on brain stem stimulation. In looking at these individuals I will make related points about respectively: firstly the establishment of large cages in Oxford and the shifts that this led to in the type of work performed, secondly examining the relationship between field and laboratory, and thirdly examining the new vivisectionist approach that was tried in this later laboratory situation.

Section 2.1 Morris, laboratory studies of bird behaviour, and serendipity,

Desmond Morris remained at Tinbergen's laboratory for two years after he finished his D.Phil., leaving for a job at Granada Television in 1956 for the *Zootime* programme based in London Zoo that would make him a household name in Britain for the rest of the decade.[157] His later work is contemporary with the end of Moynihan's time in Oxford and the beginning of Esther Cullen's fieldwork. His research continued until he departed Oxford for London, describing in his own effervescent style: 'Working day and night, I somehow managed to write a fifty–page paper on my finches. I was still tapping away at my typewriter as the removal men began to strip the house. My desk was the last object to go through the door.' (Morris, 2006:128). Studying birds though was quite a departure for Morris, who had previously focused on sticklebacks, as we have seen in previous chapters. Morris's work is interesting not just because it was the first substantial laboratory work on

157Morris continued to write and publish his academic work for a further 2 years , which explains why he published later stickleback work in 1958.

birds by the Tinbergians, but also because it has such strong continuities with earlier Tinbergian work. Morris's work also shows the extent to which it was possible to stretch the concept of 'natural behaviour', identifying natural behaviours under the most unnatural of circumstances.

Morris's studies on zebra finches were a departure for him personally especially as he was, unusually for a Tinbergian, more of a general wildlife enthusiast than a bird–lover. His finch studies did borrow on ideas first presented by Robert Hinde, in his studies of the chaffinch, (which despite the name are related only at the level of zoological order), for example explaining and comparing the behaviour of 'supplanting attacks' in his zebra finches with Hinde's chaffinches:

> Supplanting attacks are common in situations where one bird is dominant to another. The subordinate bird flees from the spot it occupied as the dominant one approaches. This may occur repeatedly in rapid succession resulting in a prolonged chase from branch to branch. If a subordinate bird is hit it is either pecked with a closed beak, or it is snapped at. If, in the latter case, the dominant bird successfully catches hold of the other's plumage, a plucking may ensue. Owing to the speed of the movements it is difficult to be absolutely certain whether the dominant bird makes active plucking movements, or whether the subordinate bird plucks

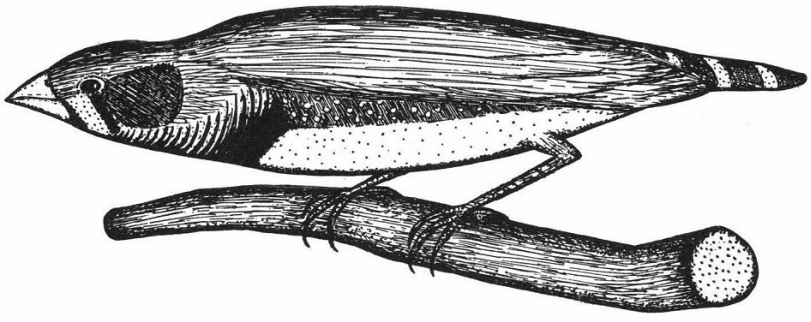


Fig. 1. A male Zebra Finch in the sleeked horizontal posture. A dominant bird takes up this posture when facing a rival.

[Image inserted as 24]

itself in its struggle to flee from the firm grip of its rival. It seems most

> probable that it is the fleeing of the caught bird which is the more important factor, especially in the light of the following observation. One male had snapped at and seized another by its wing. The next moment, the captor was hanging in mid–air from the wing of the attacked bird. The latter still clung to a branch. The captor made no attempt to fly off and thus tug out the feathers it was holding in its beak. Instead, it simply hung by its beak until the weight of its body and the captive's attempts at fleeing tore loose the feathers it was holding and, amid a cloud of feathers, it crashed down onto the top of a nest below. Not all pluckings are as spectacular as this, but, after one incident on the ground, the victor was seen to hop about collecting up in its beak a number of the feathers which it had just extracted from its rival. Then, sitting on a low branch, it began nibbling them, turning them back and forth with its tongue as it did so. After a while it let them drop, wiped its beak, and went about its business. The significance of this pattern is not understood. (Morris, 1954: 273–4)

Morris describes a pattern he admits that he does not fully understand. Interestingly he seeks explanations for his observations in the idea of 'supplanting attacks', which were first observed and described by Hinde in his fieldwork, showing how a laboratory worker could happily make use of a concept originating in *fieldwork* directly, something that many other laboratory animal researchers, especially Behaviorists, would not have done. Elsewhere in the article he references his own laboratory observations on sticklebacks (e.g. Morris, 1954: 294–5, where he references Morris, 1951). In his practice then, Morris was prepared to make use of observations derived from both the field and the laboratory. He was also comfortable in applying observations or analysis from one species in the laboratory to another suggesting that neither species barrier nor location was a major concern in the choice of whether to apply a theory or not.

The observations above by Morris were the consequence of deliberate choices he had made to interfere in the lives of his finches, by placing them in specially designed

cages, so as to see what would stimulate certain behaviours. Describing his methods of studying the Zebra finch he states:

> The birds were housed in wire aviaries with dimensions of approximately 4 x 3 x 2 feet. Dense clumps of twigs were fixed in the corners of these to provide nesting sites. Nesting material, in the form of straw, grass and string, was scattered over the floor. Each aviary was screened from all the others. Wire passages which could be opened and closed by a panel, were inserted between certain of the aviaries (see Fig. 11 [image 25]). These were used in the study of territorial behaviour. (Morris, 1954: 272)

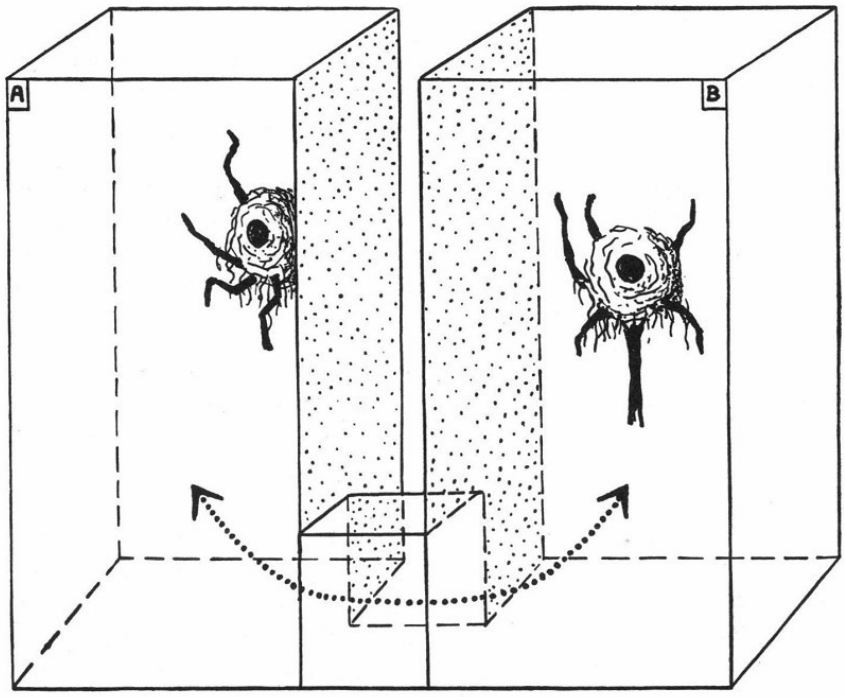


Fig. 11. Aviaries A and B, in each of which a nest has been built, showing the linking passage inserted between them. This passage could be opened or closed by a panel and was used in studying territorial behaviour. The dotted surfaces of the aviaries were opaque, as was the panel, so that, when the latter was in place, the birds in A and B were unable to see one another. The dotted line shows the flight path between the two aviaries when the passage was opened.

[Image inserted as 25] (Morris, 1954: 313)[158]

Morris chose therefore to study territorial behaviour by placing birds in these conjoined aviaries, and observing as gateway was opened and closed. In doing this

158The sharp–eyed reader will note the discrepancy in page number between the quotation and the picture, which came much later in the article. As Morris chose to direct his reader there I have reproduced it directly below the text, rather than reprint the majority of the original work.

he could easily see what stimulated certain behaviours associated with territoriality – recalling directly his earlier studies on stickleback territories. Clearly this is a more interventionist way of studying territory, as it relies on choosing to allow or disallow passage from one territory into another, something that was not true for the stickleback studies, in which he merely observed their behaviour and inferred their territories from that. However in these finch studies it was still his intention to elicit the natural behaviours associated with territoriality, by this interference in their lives. This is in stark contrast to his observations on on Java sparrows, (from the same Estrildidae family as the zebra finch), which arose as the unintended consequence of placing them in winter quarters with necklace doves (Morris, 1979: 101–105). Morris's rather peculiar observations are as follows:

> The Necklace Doves in my own observation, were not incubating and had no nest, but the Java Sparrows were nevertheless seen to be attracted to them, and the following interspecific patterns were observed to occur:
>
> 1. A Java Sparrow was frequently seen to sit next to a Dove in preference for a member of its own species (Fig. 2 [image 26]).

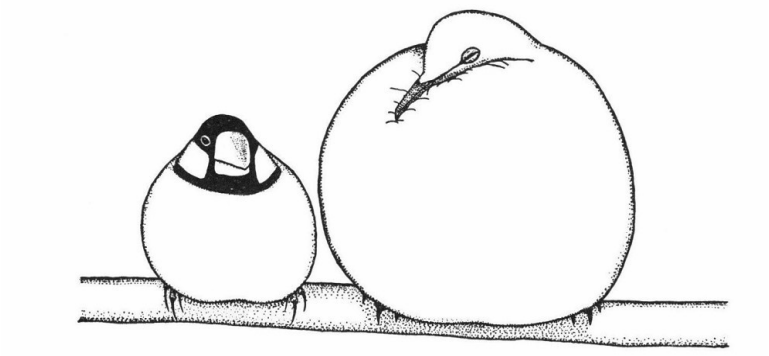
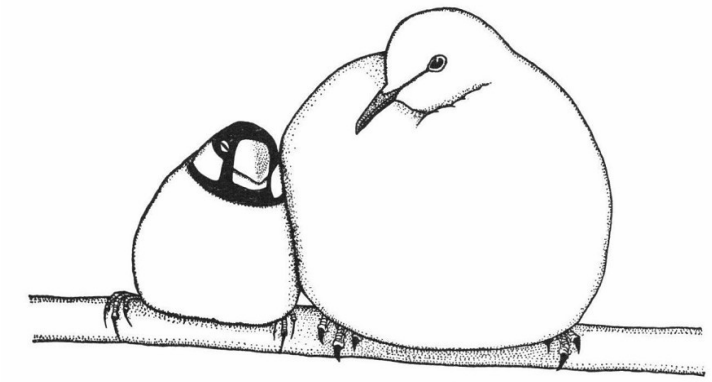


Fig. 2. The Java Sparrow — Dove relationship. The finches were strongly attracted to the doves and not only sat with them, as shown here, but also performed various other social activies with them. For explanation, see text.

[image inserted as 26]



Fif. 3. A Java Sparrow clumping alongside a Dove.

[Image inserted as 27]

2. On a number of occasions a Java Sparrow was seen to push up against, or to lean against, a Dove (Fig 3. [image 27])

3. A Java Sparrow was seen to push up between the legs of a Dove and plunge itself into the ventral plumage of the latter (Fig 4. [image 28 higher]). Once, at dusk two Doves were seen sitting near one another, with no Java Sparrows in sight. The slight disturbance caused by the presence of the observer resulted in the appearance from beneath each Dove of the head of a Java Sparrow.

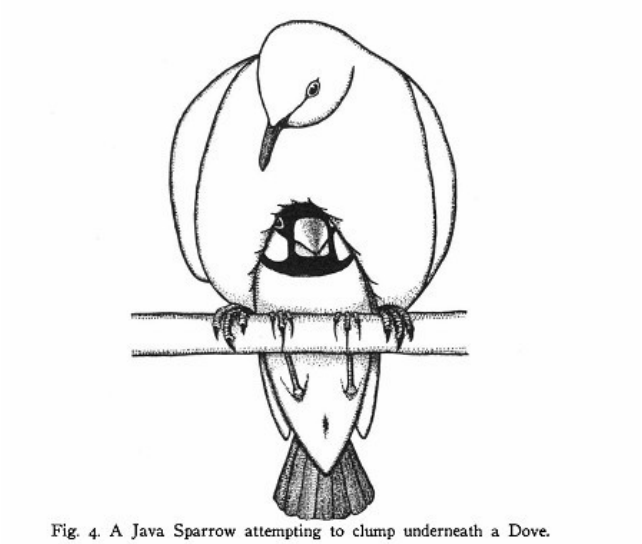


Fig. 4. A Java Sparrow attempting to clump underneath a Dove.

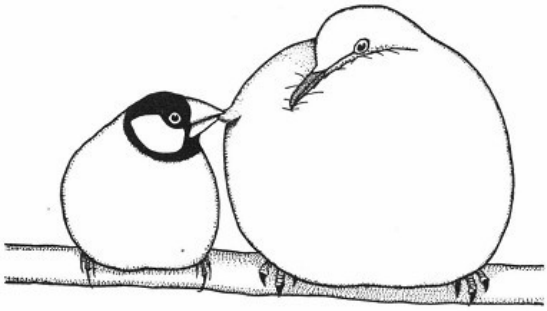


Fig. 5. A Java Sparrow preening a Dove.

[Image inserted as 28]

4. The Java Sparrows were occasionally seen to preen the Doves in preference for preening one another (Fig. 5 [image 28 lower]).

5. When the number of Java Sparrows was increased above that of the Doves, the dominant Java Sparrows defended against rivals the Doves they had selected to clump with (Fig. 6 [image 29 higher]).

6. On a few occasions, a Java Sparrow was seen to "play leap–frog" over

the back of a Dove. The latter remained in its place on the branch, whilst

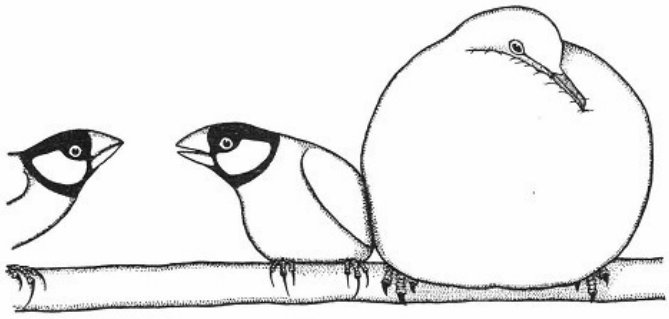


Fig. 6. A Java Sparrow defending its Dove against a rival.

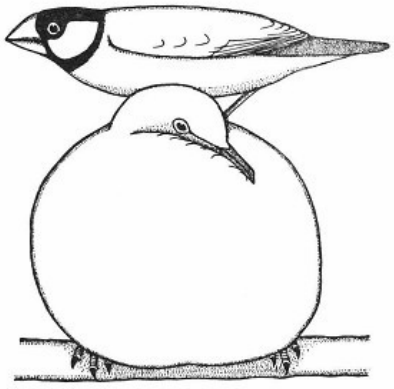


Fig. 7 A Java Sparrow "playing leap-frog" over the back of a Dove.

the Java

[Image inserted as 29]

Sparrow hopped from one side of it, onto its back , and then off again. Then it turned, hopped again onto the back of the Dove, and again hopped off the other side. This performance was then repeated several times. It should be stressed that this was not a copulation attempt since, when the Java Sparrow was mounted on the Dove, their long axes were at right angles to one another (Fig. 7 [image 29 lower]).

It has already been pointed out that one species of finch will clump with and preen an individual of another species if the latter fluffs out into the spheroid posture. It is only one step further to the Dove case. Doves, even when active present an extremely rounded appearance. When Doves assume the resting posture, it is a much larger and much rounder "spheroid" that results, when compared with that of finches. It provides, in fact, a supernormal clumping stimulus which is more attractive than even that given by other Java Sparrows. (Morris, 1956:

88–91)

Morris is happily mixing up the lives of the creatures he is studying here (and even those he is not interested in, here the poor Necklace dove). Explaining the meaning of his observations to the public in his autobiography he suggested thinking of them as saying:

> If roundedness meant 'Come sleep with me', then the Dove's super–roundedness meant COME SLEEP WITH ME! And the little sparrows were compelled to obey this signal even if it meant ignoring the fact that they were clumping with a totally alien species. (Morris, 1979: 103).

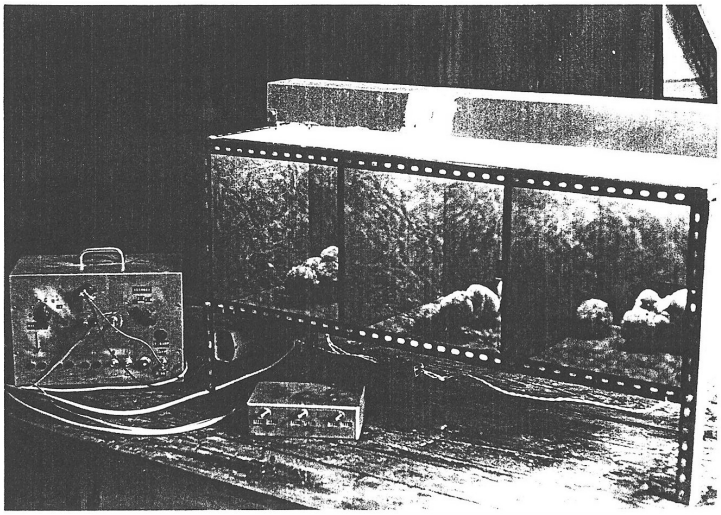
What makes this so surprising is that Morris was the person who had declared that the "rat–maze psychologists" could add nothing to knowledge of animal behaviour because of the artificial nature of experimental conditions and laboratory surroundings in which they worked. But by reporting observations which could only have occurred under laboratory conditions he was apparently doing exactly what he had previously condemned. Morris recognised the 'artificiality' (Morris, 1954: 315) of observing caged birds, and some distortions of their behaviour that had to be expected under laboratory conditions, stating for example that: 'Further observations on territorial behaviour in the laboratory are, of course, probably subject to considerable distortion, but such distortion is bound to be of a superficial nature' (Morris, 1954:312). However Morris's observations on the Java sparrow were only possible because of accidents of stimulation – unintended consequences – and yet they were treated as though the behaviour stimulated was entirely natural, if somewhat badly directed. Morris's studies generated understanding of what would stimulate the Java sparrows,[159] but what is interesting is that he wrote about them as though they were still stimulating *natural behaviours* rather than seeing these behaviours as in some way unnatural or artificial.

159In this respect Morris's work is a direct descendent of Tinbergen's Red–Spot studies (Tinbergen 1951: 30) and also Tinbergen's work on Oystercatchers, where he showed that they had a marked preference for larger eggs over smaller eggs, even to the extent that they would care more for absurdly large artificial eggs introduced by Tinbergen, as these eggs acted as 'supernormal' stimulators, that is, they stimulated the normal pattern of behaviour even more strongly than the normal stimulus.

Morris explained the strange behaviour of the Java sparrows as a consequence of a signalling mechanism: 'Despite the fact that the doves were so much bigger, their fluffed out, rounded shape appear to be an irresistible signal to the small birds.' (Morris, 1979:103) Although the mechanism is not stimulated as normal, it existence was shown because of this instance of perverse stimulation. In this respect it recalls his discovery of homosexuality amongst sticklebacks which was also an unexpected observation. That earlier observation however was under conditions which were as near natural as possible whereas this was entirely artificial in that the two birds concerned would not have met in the wild but he still felt justified in claiming the observation as one of a *natural behaviour*.

Section 2.2 Dawkins and the domestic chick

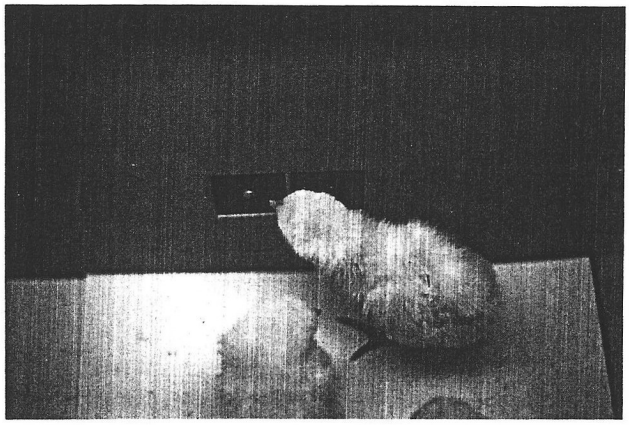
Observing such 'natural behaviour' then remained the central activity of the laboratory, but it occurred under ever more artificial conditions, as we will see by examining in turn to the work of Richard Dawkins and Juan Delius. Dawkins's work (1966) shows further shifts from the work of the early Tinbergians, though this might be not suggested by the title he chose 'Selective Pecking in the Domestic Chick.' Selective pecking in chicks was broadly the subject of Tinbergen's early red–spot tests, but Dawkins's title here suggests only a slight shift, to study a domestic animal, the domestic chick, rather than a pure wild herring gull chick. The content of the study though was substantially different from those early Tinbergian studies, with hundreds of chicks tested and highly technical laboratory experiments taking place all aimed at understanding innate decision–making processes. Dawkins, for example made use of custom–built experimental boxes:



Peck counting apparatus. Chicks are visible through the "one way screen".

[Image inserted as 30] (Dawkins, 1966: 35b)

Which when looked at up close look like this:



Peck counting apparatus: inside one compartment during a test.

[Image inserted as 31] (Dawkins, 1966:37b).

This apparatus was designed to test the chick's innate responses to a range of different stimuli. For this reason each chick was only tested once, so that they did not become accustomed to performing certain tasks. The two buttons that can be clearly seen in the second photograph above were painted in a range of different colours such as blue, red, green, orange and light green (Dawkins 1966: 40). Each of the buttons was attached to a switch which could then record which button was pressed and by counting Dawkins was able to generate tables of preferences and thus ascertain which colours were the most stimulating.

Dawkins's research was not just different in its use of apparatus from early Tinbergian bird studies. Dawkins's initial research took hundreds of chicks from a commercial farm and studied them once only under experimental conditions. Dawkins was interested in understanding what determined individual responses to certain stimuli in innate decision making processes, which is why he was interested in very young chicks rather than adult birds. Dawkins describes his experimental set up here:

> Subjects Messrs. Jennings of Garsington, near Oxford, allowed me every week to collect as many "day–old" male chicks as I wanted – usually several hundred for each experiment. The chicks were of a Light Sussex/ White Leghorn cross–bred strain. They were hatched in large incubators, sexed, and put into boxes each containing 25, in which they were transported to the laboratory. There they were kept in the light in large living areas 180 x 45 cms, at a temperature of around 30ºC, until tested. They received no food or water before testing. Their ages at time of testing ranged roughly between 12 and 60 hours. This was partly because of the spread in hatching times, and partly because my tests took place over three days. After testing they were killed, unless required for other experiments in which case they were fed.
>
> Apparatus Pecks were counted automatically by means of micro switches. The apparatus used for most of the experiments consisted of three cubical compartments, in one wall of each of which were windows through which the stimuli were presented. In earlier experiments of the series, another piece of apparatus was used, identical except in that there was only one compartment instead of three, and in that it was illuminated by an ordinary Tungsten bulb instead of a fluorescent tube. Both were largely built by Mr. Jan Adam. I am very grateful to him.
>
> Each of the cubical testing compartments had a side length of 30cms; three of the walls were painted neutral grey and the fourth served

> as a crude one– way viewing screen; screen made of black netting. A 30W fluorescent tube lay along the top of all three cubicles, shaded so much that most of its light ("daylight") fell into the cubicles. Enough of the top of the apparatus was left uncovered to allow the chicks to be put in and removed. In the wall opposite the netting screen, two 33mm square windows were cut, 3mm apart, with their tops 8.5cms above the floor. The stimulus objects appeared in the middle of these windows, mounted on rectangular plates of thin tinplate, painted black. (In earlier experiments stiff black cardboard was used instead of tinplate. Tinplate proved to be easier to clean.) These plates were held in delicate little frames, hinged at the top so that when they were pecked they swung backwards. Behind the lower rims of these hinged frames, Bulgin Microswitches (Type M, S 530) were attached. They were connected up to counters and a 48 volt supply.
>
> A large majority, though not all, of the pecks, were registered by the counters.
>
> Experimental Procedure this differed in minor details in the different experiments, but was basically as follows:
>
> Each chick was tested only once. They were tested in groups of six for five minutes. Each group of six was put in the middle of one of the three compartments of the apparatus, in nearly complete darkness. The light and the peck–counting circuit were then simultaneously switched on, and a stop–clock started. After exactly five minutes the peck counting apparatus was switched off, and the chicks discarded. The numbers of pecks registered by each of the counters was noted down, and the next lot of chicks was tested.
>
> (Dawkins, 1966: 36–38).

Dawkins is describing a laboratory experiment. That is stating the obvious, but it is, in the context of the aims and ethos of the early Tinbergians, a notable shift. Dawkins's study was intended to understand what governed innate decision–making

in chicks, and followed a hypothesis that there was a threshold above which pecking responses would always be stimulated, and below which they would not (Dawkins 1966:1). That his methodological approach was based on explicitly testing a hypothesis is also quite a shift from the early, purely observational work.[160]

It is also significant that although Dawkins is studying innate behavioural mechanisms, he is not interested in trying to replicate the natural habitat of the chicks he is studying.[161] Nevertheless in the experimental set up described the animals are merely experimental units, there is no interest in naturalising their surroundings in order that they would perform their natural behaviours. Quite the contrary, chicks are brought in vast numbers, in order to be experimented on once and then despatched. Ethologists may have been scientists who love their animals in Ewer's memorable phrase, but there is little evidence for that here. Eckhard Hess has even suggested that ethologists became ethologists because they resisted the urge to cut up their animals (Hess, 1985: 183). Whilst Dawkins's approach may not have intended to kill the chicks in order to study their dead bodies, the hundreds of chicks who became experimental collateral damage certainly seem to break with the spirit of this approach, if not the exact terms. Dawkins's nuanced if somewhat xenocidal study was as far from the early Tinbergian non–interventionist studies as it is possible to be without actually cutting open his subjects of study.

Dawkins breaks quite openly the first precept of the early Tinbergians – the idea of understanding the full range of natural behaviour – which was initially aimed at compiling an ethogram, and later slipped into just making do with very long periods of observation (as in Blurton–Jones's work above) in order to understand in detail the nature of one behavioural mechanism of the animal under study. By contrast, Dawkins avoids this by building his whole thesis on a set of experiments on chicks

160 Dawkins's went even further away from the spirit of the early school as he made use of experiments which relied upon the chicks under study learning special actions in order to take part. That Dawkins contemplated using experiments which required the training of the participants shows how much the school had changed from the early days of observational studies of the Innate Releasing Mechanism. Learning was the raison d'être for the Behaviorists after all, and the Tinbergians had come into being to study the natural behaviour of animals in the wild, and even to demonstrate that it actually existed!

161 Though by choosing a domesticated animal defining exactly what 'natural habitat might suit it could lead to quite difficult questions!

for which there was no prior period of long–term observation of their wild behaviour.[162] This is particularly interesting as Dawkins was interested specifically in the natural behaviours of the chicks he was studying. His use of large numbers of chicks (which unfortunately ended in their deaths) was specifically so that he could get evidence of *natural behaviours*, demonstrated time–after–time, and in situations where there was little possibility of their being influenced by conventional forms of training or learning. Dawkins's work then, inasmuch as it aimed to study natural or innate behaviours, was a distant descendent of the early Tinbergian laboratory work. However the methods that he used were profoundly different from what had been used before by Tinbergians: firstly because of the level of intervention in the lives of the animals under study; and secondly because of the wholly different approach to testing innate behaviours by using extremely large numbers of newly hatched chicks.

Both in ethos and in practice then (if not in theoretical object), Dawkins's experiments were as almost as far from the early Tinbergians work as it is possible to conceive. Dawkins chose to study chicks out of context, but made no concessions to them in trying to naturalise their surroundings. Nor did he attempt to study their entire behaviour patterns, or even go through an extended period of observation. Rather his only contact with his animals was as brief subjects in his experiments in which rather than observing he was hypothesis–testing. However there remains the continuity that he was interested in innate rather than learned behaviour. Furthermore though one result of his work was the death of very large numbers of chicks, this was not the intention and no dissection was performed on their corpses.

Section 2.3 Delius and the Vivisectionist turn

The last student whose work I will investigate is the German–Argentinian Juan Delius whose work perhaps pushed furthest away from the ideals of the early ethologists, whilst being a project in which Tinbergen had an interest. The starkest way that Delius's work is differentiated from all previous work in the school is that it

162Perhaps because Dawkins was a such brilliant student, whom Tinbergen described as 'the best man I have taught in tutorials' (Tinbergen, 1962: Ms.Eng.c.3135/c74), he could get away with such a profoundly different project. But whatever the reason he was given astonishing leeway to stray from the traditional Tinbergian path.

was based on studies which did cut up the animals they investigated, and did so whilst they were still alive. Delius had begun as a fairly conventional field Tinbergian studying skylarks for his Ph.D. which was from Göttingen University (1961), though Tinbergen had been involved in it and had supervised the fieldwork for it at Ravenglass (Tinbergen to Mayr, March 23, 1961, HUG(FP) 14.17; Delius, 1969: 137 *footnote 1*). However Delius's post–doctoral work shifted away from the Tinbergian tradition both in methods, choice of animal and later theory. In methods Delius asked neurophysiological questions and sought to answer them through experimenting on brain–stimulation. He made use of new large aviaries and took in birds not normally associated with caged lives: herring gulls and lesser black-backed gulls. Ultimately Delius's work would lead to some serious questioning of classical Tinbergian theory as well.

The money for this rather unusual study came not from Tinbergen's usual sources, the Nature Conservancy Council and the Nuffield Foundation, but instead came directly from the United States Air Force, (Kruuk, 2003: 243), who for this reason own some of the original research (see for example Tinbergen, Vowles & Delius, 1967; also Delius 1969: 137 *footnote 1*). Entirely what the reason for the U.S. Air Force's interest in brain–stem studies was is not clear from either Tinbergen's letters or from the archive material that remains, so I can only surmise that they had an interest in the physiology of behaviour during flight; Kruuk suggests this is because of an expectation that these studies would 'open up our understanding of the motivation of animals, and our causal analysis of behaviour.' (Kruuk, 2003: 243). Precisely what the pay-off for the U.S. Air Force Office of Scientific Research (European Office of Aerospace Research) would be, however, remains unclear.[163] The studies themselves however do provide us with an example of another direction that the Tinbergians laboratory took in the later period. In the extract below Kruuk describes the set–up of the experiments using material from an interview he had with Delius:

163In a letter to Ernst Mayr Tinbergen tells Mayr that he has a grant for £50,000 for Delius's studies, but neglects to tell him where the money originates from. By contrast he happily reports that the Nature Conservancy Council gave him a large grant of money, enough that it would keep him going until his retirement. This suggests to me that he *consciously chose* to cloud the origin of Delius's grant. See Tinbergen to Mayr March 23, 1961, HUG(FP) 14.17.

He appointed his former PhD student Juan Delius to lead it, Dick Brown to do the fieldwork in the gull colony, and some assistants. Just as in the appointment of students, there was no advertising of positions; things were not done that way in those days. Niko knew a person whom he thought suitable or likeable, and took him or her on. Large aviaries were erected in the garden on Bevington Road[164] with a population of 50 young herring gulls; experiments aimed to stimulate given parts of their brains with micro–electrodes and to measure their behaviour, and to provide a comparison of this with behaviour in the field.

The project was beset by problems from the beginning. The neighbours complained about the very noisy and smelly gulls (not surprisingly, in suburban Oxford), the university had no planning permission to erect cages (but it was granted later), and the adult gulls were too wild and kept bashing themselves against the sides of the cages. So the researchers had to work with juvenile gulls only, and these did not show any of the displays that one sees in the colony. Even the young birds often shook the electrodes off their heads. Dick went his own way in the fieldwork, and there was no collaboration with Juan. Niko lost interest fairly soon after the project had started, leaving it all to his juniors to sort out.

Even more dispiriting for Niko was that the few results of the electrical brain stimulation were totally unexpected, and bore no relationship to his theoretical framework for behaviour. For instance, the classical, *The Study of Instinct* hypothesis about threat behaviour was that it was a conflict, a mixture of aggression and fear. Niko expected that there would be a 'fear centre' in the brain, and an 'aggression centre': stimulate either of them with electrodes and the bird would attack or flee, stimulate both of them simultaneously and one expected threat behaviour. What happened was that Juan with his electrodes could elicit clear threat behaviour, also clear fear behaviour, but no aggression. When stimulation

164This was the site of the building owned by the ABRG, a converted house.

> elicited threat, if the bird saw something that usually produced a slight fright, the result was all–out aggression.[165] It was all quite inexplicable and this, together with the theoretical problems of behaviour motivation... was for Niko, another nail in the coffin of causation studies. After four years of brain stimulation Juan had enough, and the project was abandoned. (Kruuk, 2003: 243–244).

The rise and fall of these brain–stem stimulation studies was evidently rapid and after their failure Delius moved away from Oxford University, first to Durham University, and then to University of California San Diego (UCSD). The methods used remain an interesting case study particularly as Tinbergen's original plan incorporated both a fieldwork and a laboratory aspect, demonstrating how tightly Tinbergen thought the two research sites might have been able to cooperate. The fact that the field aspect of the project quickly faded may show the limitations of the practical space for overlap relative to the aspiration. Kruuk points out one key problem was that in the aviary the gulls simply did not behave in the natural way that they had expected. On the one hand the adults were 'too wild', and threw themselves against the cage bars, and on the other hand the juvenile birds which were brought into replace them failed to exhibit natural behaviour seen in the wild. For an early Tinbergian this should have been an absolute impasse. The early Tinbergians had sought to watch nature in as natural a set of surroundings as possible, in order that they could watch as natural a set of behaviours as possible. That the later aviaries were making the birds uncomfortable and uncooperative in behaviour terms would have made them antithetical to the early Tinbergian approach. Virtually Delius's entire experimental set–up would have been profoundly out–of–place to the early Tinbergians. His experiments involved partially tamed birds being hand reared in order that they could be surgically altered and regularly handled as adults. Finally there was the surgical implantation of brain probes themselves which ran against the idea that ethologists don't cut up the animals they studied. He describes his work:

> The herring and lesser black–backed gulls (*Larus argentatus and*

165Kruuk references Delius's (1973) paper on the behaviour of juvenile gulls at this point.

> *L. fuscus*) were hand–reared from eggs, keeping them in semi–isolation for 5 weeks; this made them reasonably tame. Then they lived in large aviaries in groups of 6–8 feeding on fish, meat and dog biscuits. Water was available in small ponds. When at least 8 months old, but always before they reached sexual maturity at the age of 3 years, they were implanted under pentobarbital anaesthesia (Delius, 1966a) with up to 8 stainless steel electrodes of 0.1 mm diameter and with 0.25 mm^2 uninsulated tips. A subcutaneous bare wire served as the indifferent electrode (Delius, 1966b).[166] After a week's recovery they were tested for 10–20 sessions spread over 2–3 months in a $4m^3$ cage. During each session each electrode was stimulated several times with 50 cycles sine wave current up to 200 μA. The brains were then conventionally processed and the electrode tips localized on sections stained for fibres and cells. (Delius, 1971: 65).

A sense of just how intrusive Delius's probes were comes from the diagrams from his 'Technical Note' (Delius, 1966b). The note itself describes how to practically perform brain stimulation in small animals, but focuses on gulls, and highlights problems such as thinness of the skulls that small animals have, and how this proves a difficulty for anchoring electrodes there. One way to overcome this that they demonstrate is to drill and implant screws into the skull to which a larger plate with the electrodes can be fitted:

166Delius explains in the earlier paper, which is a technical note rather than a theoretical contribution, that it is necessary to insert both an active and indifferent electrodes for the current to flow easily.

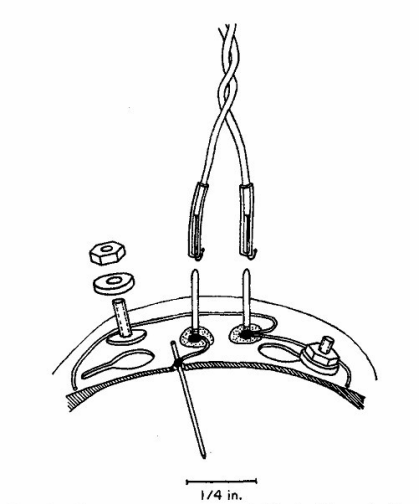


FIG. 2. Pin type connectors and "keyhole" anchoring to the skull. The layout of the indifferent electrode is also shown.

[Image inserted as 32] (Delius, 1966b: 395)

I have to confess that reading about this aspect of the research made me feel somewhat squeamish, not a feeling I had to deal with at any other time in connection with this research project. That feeling is in fact reflective of the content, as at no other time with the Tinbergians was there quite such a directly *surgical* project; instead the other subjects of study (with the noted exceptions of Dawkins's chicks, and Morris's unexpected winter–quarters observations on the Java sparrow) had either been observed in the wild, or in as natural a set of surroundings as possible. The later experiments in the lab had shifted a very long way from the original Tinbergian ideal. Delius's birds were raised in utterly unnatural surroundings, they were hand reared specifically in order that they would become tame. They were fed amongst other things, dog food, which if you recall Tinbergen's berating of Desmond Morris for feeding meal worms bought from an angling supplies shop (which I mentioned in chapter three) seems an enormous leap from the behaviour expected of a Tinbergian. Clearly the old rules did not apply, or at least not nearly as strongly.

The final section of the methods paragraph which I reproduced above states quite plainly that: 'The brains were then conventionally processed and the electrode tips localized on sections stained for fibres and cells' (Delius, 1971: 65). In layman's terms what that means is that following the long series of experiments, the gulls were killed, dissected, their brains removed and slices cut through them in order that they

could be stained and observed under a microscope, so as to locate where in the brain the electrodes were reaching. The idea of studying the whole animal's behaviour in its environment is very hard to square with the actual practices of Delius in his aviary and the attached laboratory. However even at this extreme distance from the early Tinbergian ideal the aim was that familiar one, to know more about *natural behaviour*. This is why the project was initially set up with Dick Brown[167] to do *fieldwork* on the same topic. Kruuk even suggests that Tinbergen wanted to study electrical stimulation because he wanted to see if natural behaviour patterns could be released, as they had been in chickens by Erich von Holst (Kruuk, 2003: 243). As Kruuk explains:

> He wanted to have it done with gulls, the birds about which he knew so much, in the lab as well as in the field. It would be a major link between physiology and field observation, it would show the neurological basis of the birds' motivation of their displays and of other behaviour. (Kruuk, 2003: 243)

So this was intended to be a project that found a neurophysiological platform for the behavioural responses that they had become so good at observing in the field. That it failed to do this, and indeed lost its fieldwork component quite rapidly shows that there were still differences between lab and field even though both had become increasingly interventionist and had made use of substantially similar theories until this point. Delius's focus on the neurophysiological aspect of behaviour causation could not be brought into alignment with the observation–led studies of visual stimulation–response of the early school. The phenomenon he studied however, i.e. natural behaviour – and the patterns he looked for – threat, aggression and fear – were staples of Tinbergian studies throughout the whole life of the Tinbergians. That Delius's results were not easy to fit into Tinbergian theory must have been a disappointment for Tinbergen. In addition this was his only explicitly trans–local study, one that tried to tie field observations to laboratory experiments, an aim that it comprehensively failed to achieve. However, that Tinbergen even attempted such a

167Brown was replaced by David Vowles, which is why Vowles appears on the publication list and not Brown.

unified project suggests that he saw the field–laboratory divide as something that it would be possible to bridge, and this is supported by the enormous amount of movement both of people across the field–laboratory boundary, and also the enormous movement of methods, observations, theories and analyses.

Conclusion

The main themes of this chapter have been change over time in the field and laboratory research. We have seen how there were strong similarities in the trajectories of research undertaken in the two arenas. The main similarities emerged from three things: firstly from a continuing commitment to study natural behaviour, though with constantly changing methods; secondly a trend away from general ethogram building observation and towards understanding individual behaviours in an adaptationist framework; and thirdly an ever increasing level of interaction with the subjects of study.

Particularly in comparison with the work of Moynihan from chapter two, whose work represents the apotheosis of the early school, this chapter highlights the extraordinary changes that the school underwent over this period, and yet continuities remained both with the earlier work and across the laboratory–field divide. The principal continuity emerges from the commitment to study innate as opposed to learned behaviour. Understanding natural behaviour remained the central object and driving force of the school's efforts throughout Tinbergen's time at Oxford. This commitment also went across the varied studies of all of the different students whose work we have encountered here, whether it be Esther Cullen on the cliffs in the mid 1950s or Richard Dawkins's laboratory studies of many thousands of industrially produced chicks in the mid 1960s. Contrasting the two suggests the flexibility and ingenuity in methods that Tinbergian studies allowed. For Cullen, though she never articulates the idea explicitly, 'natural behaviour' meant something like behaviour seen in nature, which is innate and adaptively significant. The innate propensities of the ground nesting gulls were demonstrated when she swapped their

eggs with the kittiwakes', to show that the ground nesting gulls' chicks were fatally unafraid of the edges of the cliffs. Underlying Dawkins's work is the idea of 'natural behaviour'; which is behaviour that the chicks perform which can be repeatedly observed on chick after chick whenever they were put into identical stimulus situations. Although his methods are quite different therefore, his underlying assumption about chick studies being one route into understanding the innate behaviours of a species is strongly similar to that of his predecessor Cullen.

Dawkins and Cullen provide a second convenient contrast in relation to my second general observation on the period, which is in the trend towards specificity of study. Cullen's work aimed at understanding the range of behaviours exhibited by her kittiwakes. In doing this she came to the conclusion that adaptation had shaped these behaviours to a tremendous degree. However that conclusion was only reached after she had inventoried the behaviours themselves. Dawkins by contrast had no such interest in the full range of the domestic chick's behaviours, indeed quite the contrary, he was interested only in what controlled a single behavioural mechanism, and what could influence their innate inclinations to peck or not peck at an artificially coloured button, in a box into which they had been placed. Most of the later school can be seen from this narrower perspective too; for example Heather McLannahan's work showed interest only in extending Cullen's own studies, in order to get much more detailed observations and analysis of kittiwake chick behaviour, in relation to the same observations made by Cullen. The picture is more complicated in relation to the work of Beer, and Kruuk and Tinbergen. They clearly followed Cullen's work, and even studied in detail one aspect of the birds' behaviours, those in relation to eggs and egg–shell removal. However their studies focussed on understanding competing selection pressures and survival value, which necessarily involved considering wide aspects of their birds' behaviour relative to its environment, and the impact of any predators.

The final aspect which was shared across the various different field and laboratory studies was a very strong trend away from purely observational studies, in favour of much more interventionist and experimental studies. This included several aspects

across field and laboratory, each highlighted by the work of different Tinbergian students. Nick Blurton–Jones for example, who went back to the site of Robert Hinde's early studies, intervened directly in the lives of the animals he was studying, and made this a focus of his work. Whereas Hinde had placed automatic recorders in the nests of his great tits, in order that he could more accurately record their comings and going, Blurton–Jones habituated his subjects to the use of a feeding table and then tested their responses to various stimuli, including stuffed predators. The difference is in both the type and extent of the intervention, Hinde's had been at a low level, and only intended as an aid to visual recording. Blurton–Jones's was central to the studies he was producing, as he altered the environment of the birds, and supplied them with a food source in order that he could apply stimuli to them, as a means of understanding their behaviour and its adaptation. Morris, though initially inadvertently, also altered the environment in which the species he was studying were living. The confused Java sparrows' responses to the necklace doves were the unintended behavioural consequence of winter housing, but these peculiar observations were completely the consequence of intervention and involvement in the lives of the birds he was studying. This is however a more complicated case as the results were not sought by experimentation, but stumbled upon by accident. Juan Delius's experiments, by contrast, very much demonstrate the outer extents of what was possible for a Tinbergian to study as natural behaviour. His work, with its vivisection, was quite at odds with much of the ethos of the early ethologists. However, given that what he wanted to do was uncover the neurophysiological mechanisms which underlay the drives that the Tinbergians had observed in the wild, it was certainly a related project. The degree of intervention in the lives of the birds under study that vivisection implied, however, is considerably greater than anything else attempted by the Tinbergians, so his work must be seen as the far extent of the trend, rather than as a standard point.

Overall the Tinbergians remained bound together by their shared interest in understanding natural behaviour, even though there was perhaps a growing methodological pluralism over the course of the school. That work as distinct and different as Delius's, and Dawkins's and something as purely field based and not at

all harmful to the lives of the birds studied as Colin Beer's, could all still be Tinbergian shows the diversity within the school. It was possible to study quite distinct behaviours, using quite distinct practical techniques, and remain in the school, as long as the central object of study, however broadly conceived, was that of natural behaviour.

Chapter Five: The Tinbergians and the Public

Introduction

True Tinbergians have never shrunk from the limelight. Whilst many did not end up as household names, that so many of them produced so much for the public marks the school out. Many of the Tinbergians had an abiding commitment to public science – to the extent that many of them produced public science works, appeared on radio, and television, and wrote articles for newspapers or journals. There are an enormous number of these books, articles and appearances running across the work of many of the school, including Tinbergen himself, Desmond and Ramona Morris, Richard Dawkins and Hans Kruuk amongst others. The sheer scale of these public works is vastly out of proportion to the size of the group, and may well have made them one of the most publicly visible groups of scientists in Britain in this era. The fact that two of these figures are still household names (Dawkins and Desmond Morris), is anomalous as few other research schools in any discipline have produced one household name scientist, and yet by the late 1970's Tinbergen's had produced three (himself included).

The scale and success that the Tinbergians' public output had (which came not without considerable controversy in places) tells us that this must have been a major part of the Tinbergians life. This makes it immediately worthy of note, but not necessarily of study. What I will argue in the first half of this chapter is that, in the public presentation of their science, the Tinbergians described their research in ways that were distinctively different from the way it was presented in their more academic output. This makes it of profound importance for my study, as I will show that Tinbergen's fieldnotes are sometimes more accurately reflected in his popular science than in his academic work. For this reason I shall examine the triangular relationship between his fieldnotes, his academic output and his popular literature in the first section of this chapter. The second section will look at Tinbergen's

motivations for writing for the public, suggesting that it helped the school in a twofold manner: firstly by publicising his methods and results; and secondly by providing public justification for the research, which was after all in receipt of public funding.

In the third section of this chapter I will consider by far the most controversial aspects of Tinbergian school literature and output – that which concerns humans. It was this later output by Desmond Morris (The Naked Ape, 1968) and Tinbergen's own Autistic Children (1983, with his wife E.A. Tinbergen) that landed them in considerable controversy, if for very different reasons.[168] The controversy that followed Morris and later also Dawkins (whose writing was not principally concerned with humans), arose particularly from conflict with those in the social sciences and the humanities particularly in "the Sociobiology Debate"[169] of the 1970's. Anti–Sociobiology groups often attacked Morris and Dawkins, and even Tinbergen, on the grounds that their willingness to talk about human behaviour in biological terms identified them as part of the long heritage of "Nazi" or eugenic or other racial science. I will argue, however, ,that such talk was actually perfectly common in the late 1960s or early 1970s. Indeed, Tinbergen's discussions of human behaviour were continuous with interests he had actually pursued since the 1950s, without the slightest whiff of controversy. I will argue that humans had always been considered part of the Tinbergian project, albeit not a hugely important one in terms of the practical orientation of their research. Rather I will argue that the Tinbergian focus on *social drama* was essential to their project of studying *natural behaviour* in the field, and that just as they saw and analysed social drama in the field, it is hardly surprising that they saw human behaviour in a similar light, since social drama is an inescapable part of human life. I will go further, to suggest that just as

168The Autistic Children controversy is described in considerable detail by Kruuk (2003: 274–279), who ascribes it in large parts to the rather aggressive tone of Tinbergen's book, plus the increasing evidence that autism was genetic and congenital, which implied that Tinbergen's suggestions about the possibility of a 'holding cure', or a social cure were merely 'treating one of the symptoms of autism (social relationships)' (Kruuk, 2003:278).

169 The Sociobiology debate has of course been much discussed in both the academic and popular press. One of the best all–round introductions to the topic is the sociologist Ullica Segerstråle's account *Defenders of the Truth: The Sociobiology Debate* (2000). She covers the accounts of many of the leading participants, including scientists on both sides, and also actors in the debate external to science including feminists and Marxist activists of the era.

anthropomorphic thinking had been a part of their observations on animals, anthropomorphic observations of animals in turn became a part of the way that they understood humans, something we will see in the final section. Moreover, there was from early on a determination to talk to the public and to be seen as producing useful knowledge rather than merely being of narrow interest to amateurs and hobbyists. As we will see later in the chapter, Tinbergen would suggest arenas to which his methods or results might contribute, including psychiatry and psychology, and even public, social and environmental policy. To that utilitarian end, the Tinbergians showed an interest in understanding human behaviour. In order to be of practical utility, their results had to be publicly communicated, something that the Tinbergians did as a matter of course for all of their other work, but which would lead them into considerably more controversy when their gaze was on humanity.

Section 1: Tinbergian Public Communication of their Animal Behaviour Research

Tinbergen was always concerned with conveying to the public both the results of his school's endeavours and a sense of how their research was done. In this section I will show that his field practices were sometimes more accurately described in his popular science than in his academic literature. This will rely upon three–way comparison, between fieldnotes, academic literature, and his various forms of popular output, including broadcasts, but initially beginning with his most popular books. [170]

Section 1.1 Field description as it appeared in the academic literature

The field descriptions that Tinbergen reported in the academic literature were very dry. As I will argue later, his academic writing represents an abstraction from the way

170 Kruuk, in his biography of Tinbergen, gives the impression that popularisation was a characteristic feature of the later Tinbergians of the 1960's: 'Popularising his science was one aspect of Niko's career that became ever more prominent during the 1960s' (Kruuk, 2003: 252). As I will largely take examples from the 1950's I hope to shift this view, to instead show that popularisation was always a part of the Tinbergen picture.

things were done in the field. Tinbergen and his students in their academic writings give periodic examples of "fieldnotes" inserted into the main prose of the articles and theses. Partly this was to illustrate how the observations that he was analysing were made. However these passages have a further, less easily definable quality as well. To someone of an anthropological background such as myself, they give the text an almost ethnographic quality, seeming to lend the wider articles *field–derived authenticity*. These inserted passages were often though not exclusively included in the methods sections and can be found both in his and his students' work. In both situations they convey the impression of being relatively raw data. For example here is an example from Moynihan's thesis:

> A good example of redirected aggressive response to female Food–begging is shown in the following extract from fieldnotes.
>
> "Scoulton. March 18, 1952. 4:17 p.m.
>
> Watching a pair of birds floating on the Mere. The two birds are swimming parallel with one another. Both do Oblique – Forward – Upright – Head–flagging. The male then swims along in the Upright. The female begins Food–begging very energetically. (she is in the Hunched Posture, but she still shows a trace of Head–bobbing). There is no apparent response by the male.
>
> The female flies up. A very fast, circular, flight (she does not chase other gulls, but she gives the Long Call).
>
> The female comes back to the male, again they both swim along parallel with one another, and again they show Forward – Upright and Head–flagging. The female starts to beg again, and the male takes evasive action.
>
> The male flies off suddenly and dashes at his neighbours. He screams the Attack Call. The neighbours leave, and he settles down. (Moynihan, 1954: 152).

The passage above is a representative example of the published "fieldnotes" of a Tinbergian: Moynihan's thesis, for example, has similar extracts on pages 153, 157,

158. It begins with the place, date and time, and is filled with classic Tinbergian posture descriptions, identified by their capitalised first letters: Oblique – Forward – Upright – Head–flagging. This passage then conveys the posture–by–posture approach of the classic early Tinbergian work. Moynihan typed this passage, like his quotations from other people's work, in a single–space font, whereas the body of the thesis is double spaced. This gives the impression that this text is of a different character – more akin to his observational diagrams – than to the main body of the text. Indeed this analogy can be taken further in that, as with his use of observational diagrams, his reports are not interrupted, and analysis is kept separate, beginning only on a later page of the thesis.[171] Moynihan's format was different when he wrote for the journal Behaviour, as his context markers had been removed or placed in the main text, as in the following passage:

> There is, for instance, the following entry in field notes of May 17, 1952:
> "The female forces the male off the nest 3:48:00 p.m. The male walks off a foot or so. He then preens steadily and vigorously. The male walks back to the nest 3:50:30. He sits down right beside the female, pushes her, and finally forces her off the nest 3:51:02. The female walks a foot or so away, preens for a few seconds, then walks away a few feet further."
> Similar incidents are not uncommon. In such cases, it is hard to avoid the conclusion that the incubation drive, of the bird momentarily leaving the nest, has remained high throughout. (Moynihan, 1953: 72)

This is the format he uses as standard throughout his Behaviour publication (c.f. Moynihan 1952: 61), where the date has been moved to the main text and the location of the observation entirely removed. Interestingly the time is recorded far more accurately than in the previous passage, but that is the only way that the detail has been extended. Overall the visual conventions are maintained, in that the "fieldnotes" are kept separate from the text around them. The two passages are very similar in form, if not in the content of the observations that they contain. Both are

171 His analysis which followed a few pages later begins by explicitly bracketing off motivation and function: 'I will not attempt to analyse, here, the motivation or function of Foodbegging by the female, or of regurgitation by the male.' He discusses it purely in terms of external stimulation and context, as we would expect of pre–Esther Cullen fieldwork.

almost posture–by–posture accounts, but the second is a much briefer extract, and therefore has a reduced amount of observational detail.

Regardless of the minor differences between the two Moynihan passages above, in both examples it would appear that the fieldnotes were inserted to give more authority to the passage in which they were contained. The events described in them could easily have been paraphrased or described without breaking the flow of the text. They add an extra–scientific "I was there" element, as much as any intrinsic merit they may have as "data". This type of "fieldnote" is quite common in many of the Tinbergian publications for an academic audience, indeed Tinbergen used it in his 'Comparative Studies of the Behaviour of Gulls (Laridae)' paper (1958b), in which he made use not only of his own "fieldnotes", but also those of Esther Cullen (Tinbergen, 1958b:23). The reason that I have put "fieldnotes" in quotation marks in this section is that I do not believe these insertions accurately represent the fieldnotes as they were recorded in the field. The reason that I state this is that though we cannot compare all the "fieldnotes" as they were published in the academic literature with the notes made in the field, largely because many of them have been lost, where we can compare the two there are significant discrepancies, as we will see in the next section.

Section 1.2 Contrasting the published academic accounts with the fieldnotes

If the tale of Casanova discussed in chapter one has taught us anything, it is that Tinbergen's fieldnotes are often not what we expect them to be. This is especially true in the rare occasions where we can contrast his "fieldnotes" as they were written up for academic and scientific publication with the original fieldnotes themselves. Precisely why Tinbergen chose to give 'extracts' to his academic readers is unclear – though it may perhaps reflect the influence of earlier field naturalists, such as Edmund Selous, who published their field diaries at length (e.g. Selous, 1927). As I suggested in the previous section however, I feel that the principal reason for inserting "fieldnotes" was to convey a sense of field–derived authenticity. Regardless

of what the immediate cause was, Tinbergen made considerable use of these "fieldnotes" in his academic publications, for instance in this example:

> March 10, 1957. Ravenglass. Two Black–headed Gulls are observed feeding on a gravel bank in the estuary. They are obviously a mated pair. While feeding they wander apart, the male feeding on one side of the bank, the female on the other. Thus the birds are usually separated by the bank, which is about 3 ft high. In the course of 70 minutes the male performs the Oblique–cum–Long–Call 16 times while the female is out of sight. These calls are responses to other birds approaching him. In 13 out of these 16 cases the female runs up to the male immediately when he calls. [On the other three occasions when she failed to do so she was herself engaged in a squabble with another bird]. Such observations, compared with the absence of a response from the female when the male was not calling, can be made repeatedly if the observer is alert to the possibilities: they allow one to conclude that the Oblique–cum–Long–Call makes the female approach the male. In this particular case, it was obviously the sound itself and not visual stimuli which attracted her. (Tinbergen, 1958b:23)

This observation report, was included in Tinbergen's influential 'Comparative Studies of the Behaviour of Gulls (Laridae): A Progress Report' (1958b). I read this article before I read Tinbergen's fieldnotes. It is typical of how Tinbergen generally presented his fieldnotes in his published work I initially assumed therefore that it accurately reproduced what I would find in his fieldnotes. It was written in exactly the manner I had come to expect of Tinbergian published scientific accounts: clear, direct and without embellishment. Adding the date and place of the observation, and shrinking the font to give it a different appearance to the rest of the text, further added to the impression that these were standard notes reproduced here as they were made in the field. Tinbergen's insertion of a sentence in square brackets in the middle of the passage reinforced the idea that the text outside those brackets was essentially unadulterated from the field original. In addition Tinbergen introduced this passage

from his fieldnotes by suggesting that they were a good example of his observation style.[172]

His actual fieldnotes on the same observations however tell quite a different tale. It turns out that the published version contains a large number of changes which are neither indicated nor explained to the reader of the published account. Furthermore there are no indications in the fieldnotes or anywhere else of the reasons for these changes. Here then is the original account from Tinbergen's archived fieldnotes:

> 10 March 1957
> Dull, wind warm, S, Light to moderate, light showers. Heavily clouded to overcast.
> First 7.30–9.30 on shore opposite Ravenglass.
> Young greater Blackback (1 year) had a mussel or something like it. Dropped it 9 times: first on sand, then on sand + gravel, then on pebble beach, back to sand, in water, back to pebble beach, again back to sand, abandoned it. No orientation whatsoever.
> Watched (with Colin) one firmly mated pair of Black–headed for over 20 mins. ♀ not very afraid, dared approach him[173] to almost touching. Usual greeting ceremonies (except sometimes forward omitted), ♀flew off occasionally, ♂ often (always attacking others, swooping & soaring even "in vacuo", twice on 2 Herring Gulls. When ♂ called long call in oblique and ♀ happened to be a couple of yards away in 10 out of 15 observed cases she ran (or if beyond 20 yds or so – flew) toward him, although it was clear from his orientation that he was reacting to a third bird in flight. Beautiful demonstration of the compelling attraction of "song". Of the 5 non–response occasions 2 were "failures" because ♀ was just attacking another bird on her own. The three others I can't explain – got the impression that she was keenest to come if she had been separated for some time. We watched carefully and it was clear that his long call+obl.

172 The actual quote is: 'While it would be beyond the scope of this paper to present detailed evidence on each display discussed, a few examples of the type of observation will be given.' (Tinbergen 1958b:23)

173 I presume by "him" Tinbergen means Colin Beer.

> began before she approached – in other words, she was responding to him & not the other way round. Tinbergen (1957, MS.Eng.d.2387)

The differences between the original and published version of the same observation are surprisingly large. I counted eight significant changes.[174] Some of these changes can be explained as merely edits for length and relevance, such as omitting accounts of the weather, the exact location and the behaviour of the greater black–backed gull (though presumably the greater black–backed gull could have been an important stimulus had Tinbergen observed anything he understood as a response to it). However other cuts greatly affect the meaning of the piece. One significant effect of the changes is to substantially alter the tone. 'Beautiful demonstrations of the compelling attraction of song,' in the original, is transformed into: 'it was obviously the sound itself and not visual stimuli which attracted her' for the benefit of his scientific and academic audience. The birds observed in the fieldnotes seem to be far more vital: one is *keenest* to come when separated for a while from her mate; her mate is described as *swooping and soaring*, while in the original one of the birds watched is noted to be almost touching Colin (presumably Beer), and *daring* to do it. All this adds to the impression of these observed animals being living creatures, far away from being the cold stimuli–motivated automata of his scientific papers.

The subtraction of the observer is another key difference. In the fieldnotes, Tinbergen and Beer are both present as active observers. In the academic writing, by contrast, the objectivist passive voice is maintained and no inkling of the observer as a participant is allowed. The birds merely behave and that behaviour is recorded. One layer of complexity is removed therefore with the subtraction of observer–observed interaction. Another layer of complexity, though of a profoundly different character

174 In the order that they appear in the text they are: firstly the description of the day's weather is removed. Secondly Tinbergen alters the description of the location of the birds he is observing, writing only 'gravel bank' in the published version, whereas in the original there is sand, gravel and a pebble beach. Thirdly the location of the observers is changed, from 'opposite Ravenglass' in the original text to 'Ravenglass' in the published account. Fourthly the description of the greater black–backed gull is excised completely. Fifthly Colin Beer and his brief interaction with the gull (or more correctly its interaction with him) was removed. Sixthly numbers of observations were changed, from 10 out of 15 gull observations in the original being explicable to 13 out of 16 in the published account. Seventhly the description "Beautiful demonstration" was removed. Eighthly the idea of likelihood was removed with the cutting of the phrase 'keenest to come', which had implied that there was variation in the quality of responses even above and below a threshold.

is subtracted with the removal of the possibility of likelihood and relative 'keenness' to come when called. What was left in the published account was merely a stimulus–response description, where the female bird came in response to the call, or did not come if she was engaged at that moment with another bird.

I have no explanation for the numerical discrepancy between the observations in the two passages: why 10 out of 15 instances of female following the male call are recorded in the fieldnotes, but 13 out of 16 are claimed in his published paper – certainly he doesn't record a further instance in his fieldnotes. Of course there could be a lost insert or missing piece of paper. However transforming 10 out of 15 into 13 out of 16 needs not only a further observation, but also a reclassification of at least two instances, perhaps something he was beginning in the notes by suggesting that because two of the times the female was attacking other birds those instances can be counted in either camp. In the absence of any further explanation all we can infer is that Tinbergen changed the number without telling his audience.

The large number of changes between the fieldnotes themselves and the academic literature's reporting of "fieldnotes" is interesting as a phenomenon in itself. In the light of the way that Tinbergen presents these fieldnote passages as 'data' this is even more significant. This is because it shows that Tinbergen is transforming his data quite radically for publication, even when it is presented as relatively raw "fieldnotes". This transformation meant a considerable "cleaning" of the data: removing observer–observed interactions; removing possible stimuli, like other birds or the weather; and removing complexity indicated by the degree of responsiveness. It also meant a pruning of the language of the observations – from the vivid to the mechanistic – once again demonstrating that, figuratively speaking, Tinbergen observed in colour but reported in monochrome. At least, that was true of their academic output. However, as we shall see in the following section, their public science contained some of the original *joie de vivre*.

Section 1.3 Contrasting the popular science with the academic output

Tinbergen's Social Behaviour in Animals (1953) aimed to convey some of the approach to behaviour introduced by The Study of Instinct (1951) to a wider lay public and amateur audience. Social Behaviour includes a number of illustrations both written and visual that come directly from the academic work, including the "courtship dance of the stickleback" that we saw in chapter three. In the formal academic analysis of The Study of Instinct, Tinbergen explains the behaviour concisely using his model of the "innate releasing mechanism":

> The male's first reaction, the zigzag dance, is dependent on a visual stimulus from the female, in which, as already mentioned, the sign stimuli 'swollen abdomen' and the special movement play a part. The female reacts to the red colour of the male to turn round and to swim rapidly towards him. This movement induces the male to turn round and to swim rapidly to the nest. This in turn entices the female to follow him, thereby stimulating the male to point its head into the entrance. His behaviour now releases the female's next reaction: she enters the nest. (Tinbergen, 1951: 48)

This is a demonstration of the stimulus–response description of natural behaviour, with each stage of the courtship ritual described in unemotional cause–and–effect language. The sense of the sticklebacks as instinct–driven automata is hard to escape: the swollen abdomen stimulates the male to zigzag, the red displayed by the zigzag stimulates the female, and so on. This is the classic mechanomorphic description of the type described by Eileen Crist (which I discussed in chapter one). There is no life, no social drama and above all no intimacy to the writing – it is the perfect illustration of the cold science of animal behaviour. The contrast to the second description of the same sequence of events which I will set out below could not be more marked. When he talks to the popular audience, Tinbergen's writing is full of life and vitality; what was a sequence of events becomes as sexually charged as any teenage disco:

> The light back and dark red underside together with the brilliant eye, now make the male extremely conspicuous. Displaying this attractive dress, the male parades up and down its territory.
>
> In the meantime the females which have not bothered about nest building at all, have developed a brilliant silvery gloss, and their bodies are heavily swollen by the bulky eggs which have developed in the ovaries. They cruise about in schools. In a good Stickleback habitat, they pass through occupied territories repeatedly during the day. Each male, if ready to receive a female, reacts to them by performing a curious dance all around them. Each dance consists of a series of leaps, during which the male first turns as if going away from the females, then abruptly turns towards them with its mouth wide open. Sometimes it may hit a female, but usually it stops in front of it, and then turns away for a new performance. The zigzag dance frightens most of the females away, but a single one may be sufficiently matured to be willing to spawn, and such a female does exactly the opposite from fleeing: it turns towards the male, at the same time adopting a more or less upright attitude. The male now immediately turns round and swims hurriedly towards the nest. The female follows it. Arrived at the nest, the male thrusts its snout into the entrance turning along its body axis, so that it lies on its side, its back towards the female, which now tries to wriggle into the nest, her head protruding from one end, the tail from the other. The male now begins to prod her tail base with his snout giving a series of quick thrusts. After some time the female begins to lift her tail, and soon she spawns. (Tinbergen 1953: 10–11)

The reader will of course be struck initially by the length of the description, it is far longer than the academic description. The difference in the type of language used is equally large, with the male stickleback "dressing up," while the females "cruise by," and finally finishing with a raunchy "thrust." Here the writing draws us into the social life of the animals in minute, but more importantly in *intimate* detail so we feel

a part of the stickleback world. Indeed when he suggests that those females who are not ready to mate are 'frightened away' he directly imputes human emotions to the animals he is describing – in this case the emotion of fear. Both of these descriptions of stickleback life – the academic and the scientific accounts – emerged from the Tinbergian laboratory. Though the two pieces use very different language, they both aim at describing and explaining the natural behaviour of the animal being studied – as we would expect for Tinbergian writing. What makes these descriptions, particularly the second one, seem even more remarkable, is the fact that they come from the austere coding and recording practices that I described in chapter three.

Section 1.4 Contrasting the field and the popular science accounts

Having contrasted Tinbergen's academic literature and his fieldnotes (in the first two sections) and his academic and popular literature (in the third section) it is logical to contrast his fieldnotes and his popular science, which is what I shall do here. We are not at this point unfamiliar with either of these writing modes, and so we should have some idea of the way that Tinbergen wrote in the field. One end of the spectrum can be seen in the unremittingly anthropomorphic tale of Casanova from chapter one, but most of the pages of notes resemble those seen in the previous two sections of this chapter.

The clearest example of a fieldnote reported incident that reached the popular audience is the chick that came in from the cold. Here we have a vignette, recounted by Tinbergen in Curious Naturalists:

> Occasionally the Cullens took a young bird into the tower, and they never had a less peripatetic guest: if put anywhere on a table it just stayed where it was. This is again useful, in fact a necessity, in a cliff dweller. (Tinbergen, 1958)

This passage, brief though it is, brings a slightly domesticated air to the study of

kittiwake chicks. The “tower” referred to in the extract was the building that they were staying in on the island of Inner Farne, which means that by taking the chicks to the tower, they were bringing the chicks to their home. This idea is reinforced by the use of the form 'guest', an anthropomorphism chosen in preference to, for instance, 'subject'. The fieldnote account further emphasises the idea that this was not a rigid scientific space directly akin to the laboratory:

> June 17 1951
> Later on day we find one gull chick just hatched (a little wet) we take it home, keep it in cardboard box on corner of stove and take number of tests with it. In the afternoon we leave it at home, which chick keeps calling distress call until we cover it with a lid of a sugar bowl, means that cover by handkerchief or even tea cloth was not enough but it must be somewhat heavier. (Tinbergen, 1951, MS.Eng.e.2749)

This fieldnote marks the time that the Cullens were bringing their non–peripatetic 'guest' home. The domesticated feel of the writing is furthered by the note that the amongst the range of domestic fixtures that they applied to the chick to calm it enough that it stopped calling out, was the sugar bowl. Tinbergen was clearly content to let his students do any tests on the birds and does not record them any more fully in his notes. Nor did he or any of his students publish the results of whatever 'tests' were performed on the sugar bowl chick, at least in any of their academic output. This means that we had only Tinbergen's brief Curious Naturalists vignette to guide us to what may have been significant research. That Esther Cullen could feel confident in her observations that kittiwake chicks do not move about in the wild may well have been partly due to this rather endearingly uncontrolled type of science.

Tinbergen's popular writing thus alerts us to observations made in quite an unusual way, on the kittiwake chicks that Cullen studied as a part of her famous studies. Admittedly it does not give great detail, but neither do Tinbergen's fieldnotes. It is significant that as these observations were not mentioned in Cullen's own piece

(Cullen, 1957) as a part of her general study of kittiwake adaptation, for which this could have formed a memorable example. Nor is it mentioned in Tinbergen's academic reporting of Cullen's work (Tinbergen, 1959) and so without his recounting of the vignette in Curious Naturalists, this aspect of the Tinbergians research methods would probably have been lost, or at the very least buried by being only a couple of sentences in the vast body of Tinbergen's fieldnotes. Why did Tinbergen chose to write about these 'tests' to the popular audience and not to his scientific readership? Perhaps he thought that the amateur audience would be more forgiving of non–controlled studies. He was always conscious of the audience he was writing for because he considered communication of results to be of the utmost importance, and this is something he spent time inculcating to his students, even lecturing them on how to do good scientific writing.[175] In presenting his work to a scientific audience therefore he would have been aware that describing the use of 'sugar bowl lids' and 'kitchen tables' in an experimental setting would have appeared incongruous to his intended readership. It certainly would not have lent an air of scientific respectability to his work to include in it these very domestic types of description. As the idea that kittiwake chicks are sedentary was shown by Cullen using other means, these 'tests' may have proven surplus to his requirements. By contrast when he was writing for a popular audience, these domestic features aid our comprehension; cliff–top behaviour patterns may be difficult to understand if you have never seen a kittiwake nest, but we all understand a kitchen table.

175Tinbergen gave his students advice on not just involvement in films, but also on their communication through writing, (Tinbergen, M.S. 1965). It is beyond the scope of this study to perform a literary exegesis on this whole lecture but there are two points of advice that he gives which are so compelling that it is worth relating them in full:

> Often a proverb, a popular saying, a metaphor or an analogy can be very incisive – it is often worth spending some thought on finding le mot juste. But avoid going too far; the mixed metaphor "the fascist octopus has sung its swan song" closes the reader's mind for the rest of what you say.
>
> The choice of a good title is also important. Some true–life examples: "Contributions to the breeding behaviour of the Ringed Plover": "Polygamy in a Bishop" (which the editor of *Ibis* changed to… "in a Bishop Bird."). (Tinbergen, 1973:3)

It is sadly hard to tell whether this lecture was aimed purely at his undergraduate students, but in addition to showing a breadth of literary astuteness, it also shows a dedication to clarity of presentation – qualities that Tinbergen's students were meant to infer. The point about titles brings to mind both The Naked Ape (1968) and The Selfish Gene (1976), which in their titles carry clearly and concisely the central idea that they convey to the public. Both of these books conform to the writing strictures that Tinbergen's piece suggest.

Section 1.5 Field life described in fieldnotes and popular science

One area where the fieldnotes and the popular accounts intersect quite vividly is in the wider descriptions and recordings of life in the field camps. Whilst there certainly are dissenting voices on the enjoyment and good living that was possible in the camp,[176] Tinbergen's own field accounts are very easily reconciled with his popular descriptions. His fieldnote accounts, and his popular writing, both emphasise the great pleasure it was possible to achieve by living and studying in the field, and at the same time demonstrate a constant scientific inquisitiveness which is woven into this enjoyment. This mixture of pleasure and scientific endeavour is illustrated in the following passage where Tinbergen describes what a pleasure it was to live in Ravenglass, but then moves on to consider myxomatosis and then the social organisation of gulls without pausing to separate the aesthetic from the scientific:

> Camping in Ravenglass was a delight. The sand dunes were terribly damaged by Rabbits and wind erosion, but such windswept sand hills are of a rare, rugged beauty. Since myxomatosis has swept the area, practically eliminating the Rabbits, the vegetation, particularly in the low moist valleys has staged a remarkable recovery, showing what such an area could be like in the absence of this introduced, undiscriminating, vegetarian. In the distance, the mountains of the Lake District are usually visible. Often, however, they are hidden by low–hanging rain clouds, even when the low coastal strip has relatively clear weather.

176One critic of the conditions of Tinbergian camp life, identified by Burkhardt, was the visiting American psychologist Bill Verplanck. Burkhardt describes the criticisms Verplanck made:

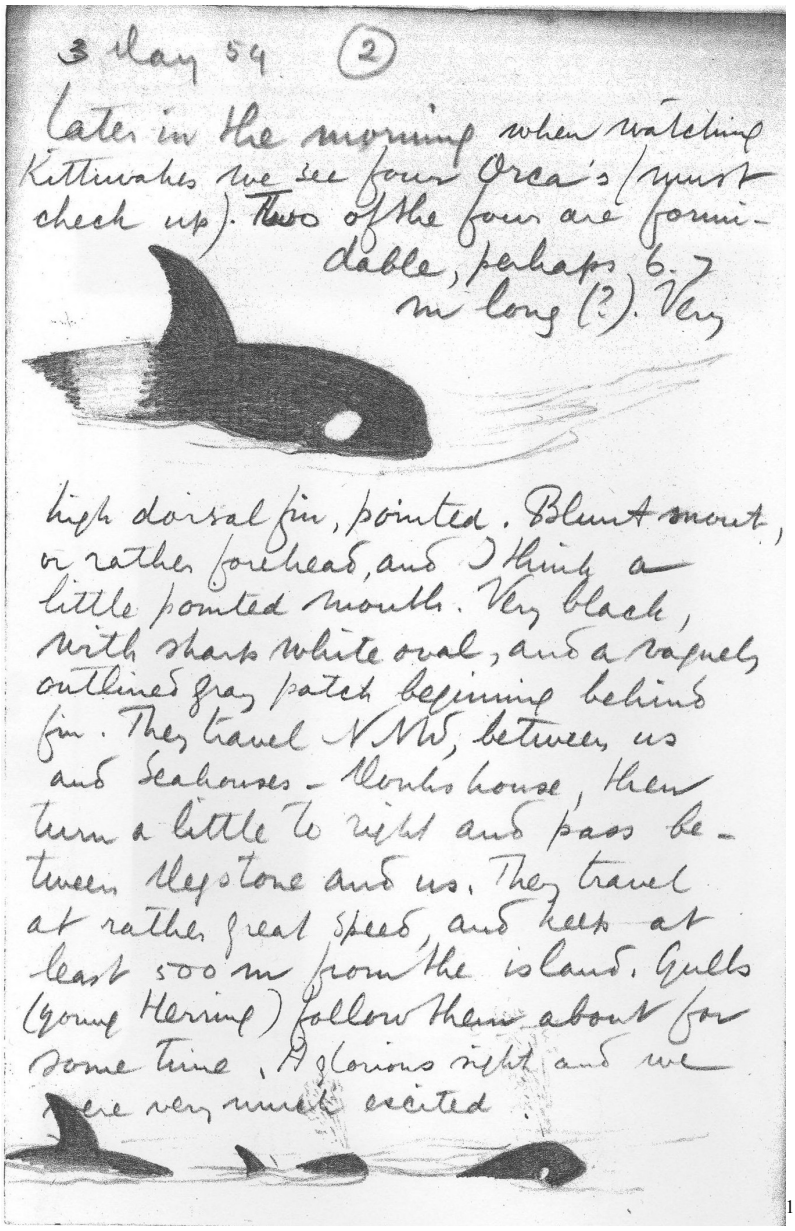
> The American psychologist Bill Verplanck, who visited Tinbergen's team on Inner Farne in late February and early March of 1953 and then later in the season described one of the beautiful days during his first stay: "Warm in the sun (Of course, warm with longhandled drawers, heavy flannel shirt, two sweaters, a muffler, a duffel coat, sheepskin gloves, and a wool hat; also heavy wool socks in the Marine boots)." He also described how the researcher's typical day began: "Up at 5:30. Shiver. Drink hot Nescafe, eat bread and marge and marmalade. Off to the cliffs on the West side of the island. Sit immobile, behind a rock, or in a hide for three hours, watching." (Burkhardt, 2005: 415)

Verplanck's manuscript is privately held, so I have not had the opportunity to view it myself. It is perhaps no accident that this visiting American Behaviorist found things not to his liking, given that so much of the Behaviorists' psychological research of the period was entirely laboratory–located, and certainly did not require dawn–chorus starts, or cliff–top observation in February!

> The general social organisation of a Black–headed Gull colony is very similar to that of Herring Gulls and Kittiwakes. The birds are obviously social, crowded together on relatively small areas even when other suitable nest sites are available all over the peninsula. Within the colony there is a a system of territories, which are the properties of individual pairs. The territories are smaller than those of Herring Gulls but larger than the ledges of Kittiwakes. (Tinbergen, 1958: 208)

Within this passage we can see a free–flowing prose style which moves between the sheer enjoyment of an outdoor life, lived on the sandy beaches at Ravenglass, and some serious scientific observations. For example he notes the changes that the myxomatosis epidemic has brought on the landscape, with the resultant positive effects on the vegetation. However even as he has finished repeating this observation, certainly a worthwhile consideration for someone interested in the interaction between environment and behaviour, he does not pause before considering the vista of distant mountains. In the next paragraph he moves directly on to consider the social arrangements of the blackheaded gull colony, and contrast it with the two other gull species studied in depth by his school up until that point, the herring gull (studied by himself) and Esther Cullen's beloved kittiwakes. He makes explicit comparative behavioural observations between these species, in a manner that fits closely with his academic writing, noting the contrasts in behaviours, and at least partially noting the difference in environments which may have contributed to the behavioural adaptations.

Tinbergen's fieldnotes contain very similar mixtures of aesthetic and scientific considerations. This suggests that when he was in the field, both of these aspects of observing nature appealed to him, if not simultaneously, then like two wellsprings from which he could draw inspiration, taking first one and then the other without pause. In one of the most telling and most beautiful passages in his fieldnotes, Tinbergen describes the joy of watching a pod of passing orcas and makes notes, diagrams and suggestions in the manner of classic naturalists since Gilbert White:


3 May 54 (2)
Later in the morning when watching
Kittiwakes we see four Orca's (must
check up). Two of the four are formi-
dable, perhaps 6-7
m long (?). Very
high dorsal fin, pointed. Blunt snout,
or rather forehead, and I think a
little pointed mouth. Very black,
with sharp white oval, and a vaguely
outlined grey patch beginning behind
fin. They travel NNW, between us
and Seahouses – Monks house, then
turn a little to right and pass be-
tween Mystone and us. They travel
at rather great speed, and keep at
least 500 m from the island. Gulls
(young Herring) follow them about for
some time. A glorious sight and we
were very much excited.

177

The sheer verve and joy that Tinbergen brings to the writing is never matched in his academic prose. The kind of all–encapsulating social drama, shown here, which includes both the studied and the studier, recalls the cheering at the gull Casanova being seen to receive his comeuppance. This kind of writing was given no place in

177 My transliteration of this passage is:

3 May 54

Later in the morning when watching kittiwake we see four Orcas (must check up). Two of the four are formidable, perhaps 6–7m long (?). very

[diagram]

high dorsal fin, pointed. Blunt snout, or rather forehead, and I think a little pointed mouth. Very black with a sharp white oval, and a vaguely outlined grey patch beginning behind fin. They travel NW between us and Seahouses – Monk's house, then turn a little to right and pass off between Mystone and us. They travel at rather great speed, and keep at least 500m from the island. Gulls (young Herring) follow them about for some time. A glorious sight and we were much excited.

the academic literature, as Crist's (1999) study showed; however it frequently reappeared in some form or other in the popular writing. Tinbergen shows his interest in recording the passing orca pod although he knows little about the species and so wishes to check. He also notes that they are being followed by juvenile herring gulls, precisely the kind of observation which might yield insights into other aspects of the gull behaviour he was studying. However to focus on the informational content is to overlook the reported excitement which is as significant a part of the fieldwork.

This kind of writing, which could enthuse an audience as much as the writing above on the delights of working at Ravenglass, is found in both the fieldnotes and the popular science, but not in the academic output. It is easy to justify expressing one's enjoyment in one's own semi–private fieldnotes, but perhaps more surprising if we consider that Tinbergen was apt to treat certain fieldnotes as 'data' which (after some tailoring) could be presented to the academic audience. This is a potentially tricky point, as it again raises the question of what the 'fieldnotes' that were found in his academic publications really were. Certainly they are not raw data – not so raw that the observer's enjoyment or pleasure in what they were watching was allowed to creep into the academic reporting of it. By contrast, as we have seen throughout this section, when Tinbergen wrote for an *amateur audience*, the enthusiasm could be left in. This still doesn't answer why Tinbergen would have chosen to write for the amateur audience at all however, and that will be the subject of the next section.

Section 2: Tinbergen's motivations to write for the public

The difference in tone between the fieldnotes and the academic literature and between the academic and the popular literature is reflective of the different intended audiences: one the scientific audience, and one the lay or popular. This section will address why Tinbergen felt the need to write for the public at all. Many scientists never do so; indeed as Morris (1979: 110) points out some risk losing status for choosing to talk to the public.[178] There are several possible reasons for writing for the

178Dealing in public science has always risked being seen as less professional by fellow professional scientists. The best demonstration of the status risks associated with public science or popularisation is given by Morris, in his autobiography, when he talks about Julian Huxley who had been a stated inspiration for Tinbergian ethologists, and who had worked in the 1920s and 1930s studying bird behaviour. Although Huxley was little active in science by the time that Tinbergen moved to Oxford, this was largely because he had become a ‘public intellectual’, and in

lay audience. One may have been that he felt it served his purposes because it communicated his findings, and his way of doing research, to far wider audiences, represented by amateur naturalists. A second reason, suggested by Kruuk, is that Tinbergen frequently took the opportunity to write for the public, and almost always set out justifications for birdwatching being a useful science, rather than merely a hobbyist's interest – something which Kruuk attributes to a sense of guilt:

> He had always had some doubts about what he had been doing, about whether it was really justified that he should spend his life out amongst nature doing what he felt like. Consequently throughout his entire scientific life he had produced justifications for his birdwatching. In fact he argued for its rights so often that a hidden sense of guilt was unmistakeable.' (Kruuk, 2003:255)

I am unconvinced by Kruuk's idea that a feeling of guilt was the prime motivating force in speaking to the public, but certainly Tinbergen did express a need to justify ethology as a science, and particularly to show that its methods and results could have practical applications. Another reason that Tinbergen wrote for the amateurs may have been to proselytise about his methods and research, and it is this one that I shall examine first, before considering Tinbergen's public justifications for ethology.

The relationship between professional and amateur naturalists was characteristically complex, particularly in the world of ornithology where there were substantial numbers of amateur enthusiasts, the best of whom had been profoundly important in the development of Tinbergen's own type of ethology. The enormous expansion of

---

the early post war era had became the first UNESCO director. Morris however is clear that Huxley's commitment to popularisation, begun only a few years prior to that of Tinbergen, was done in the face of much criticism and derision by his fellow biologists:

> He was well aware that his popularizing made him enemies, but he had no regrets on that score. And personally I was entirely on his side. I had particular admiration for the fact that Julian had been the first biologist who had dared break scientific etiquette by launching himself into the mass media. (Morris, 1979:110)

Morris of course has his own reasons for justifying popularisation as he had done a great deal of it himself, however in this passage he is justifying the work done by Julian Huxley in the face of criticism by E.B. Ford his contemporary and a great Oxford geneticist. Morris records that Ford was no supporter of popularisation: 'He disapproved of any form of popularization of his science and frowned on that part of Julian's complex character that drove him to seek a wider audience for biological discoveries and ideas.' (Morris, 1979:110).

the professional ornithology that occurred in the post–World War Two era,[179] meant that Tinbergen was fortunate as his academic research could reach many more professionals, but they were still a much smaller number than the amateur birdwatchers for example. Furthermore, his public writing played a significant role in popularising the discipline to the growing number of amateur naturalists of the period as well. His arrival in Britain coincided with a concerted effort on the part of the leading natural historians of the time to reinvigorate the subject in the public eye. In this we can point to the ornithologist James Fisher's wartime proclamation on post–war natural history – *that wildlife was part of what made the war effort worthwhile* (Fisher, 1940). Fisher was on the editorial board of the hugely successful New Naturalists book series, in which Tinbergen published The Herring Gull's World (1953b), and Fisher's drive and ethos gave the editorial board of the series much of its early impetus: 'He was a Julian Huxley for the masses; the New Naturalist incarnate' (Marren, 2005:25).[180] Fisher even published a new edition of Gilbert White's classic The Natural History of Selbourne (1947), with Fisher himself providing the introduction.[181] The early Tinbergians undoubtedly was nestled in this national milieu, though as Kruuk mentions (2003: 28–29) this is something which chimed closely with Tinbergen's Dutch background, where a similar urge to natural history prevailed.

179 Waters and Coulson make the astounding observation that: 'At the end of the 20th century, there were at least a hundred times more professional ornithologists in post in the world for every one in 1960.' (Waters and Coulson, 2003:167)

180 A sense of the extraordinary closeness of the British naturalist clique at the time can be derived from the fact that Huxley himself, as well as going off to be on the original board of UNESCO, and having been a key proto–Ethologist and later evolutionary systematist, was also the former tutor and lifelong friend of Alister Hardy who in turn was instrumental in bringing Tinbergen from Leiden to Oxford, particularly at a time when Ernst Mayr was trying to find a post for him in America (c.f. Burkhardt 2005:291–297).

181 Fisher's introduction shows just how suited the wider cultural climate was to Tinbergen's desire to use field research as a central means of building a new science of behaviour. This was published just two years prior to Tinbergen's move to Oxford, and could barely have fitted the ethos of the Tinbergians better, had Tinbergen himself written it:

> But White, if he had ever been asked why he was a naturalist, would probably have replied that it was because he liked animals better living than dead. White was a field–worker; perhaps the first naturalist who properly deserves this title, if it may be given a sense opposed to that of collector. And although he never started a "school", and although he worked as an individual and much in isolation his whole life, he was the first of many field–workers. The theory of organic evolution could have been propounded, as it was, in the middle of the nineteenth century, without two centuries or more of serious classification, and fifty years or more of serious field–observation. It was useless to know how animals were built without also knowing the quality of their lives. (Fisher, introduction to White, 1947:xiv)

Tinbergen wanted to engage with the amateur ornithological audience for reasons that he stated in his popular literature. The first is a clear enjoyment of the natural world around him, which he wanted to share with his audiences. When Tinbergen engaged with the public he also suggested the possibility of utility: he frequently tried to justify his own work as being practical and useful. In particular he suggested that by studying innate behaviours in animals we would learn lessons for man. He would even go on to suggest that the ethological method of long term observation with minimal intervention would be of considerable value in the study of human psychiatric conditions, including autism (Tinbergen, 1983:24). He also wanted to show the public how they could do field observations of bird behaviour. To this end his popular science from the very beginning gives practical how–to hints, along with the vignettes of field life, which we saw in the previous section.

Section 2.1 Teaching the ornithological world to observe as he did

Tinbergen was interested in teaching amateurs to observe bird life and particularly bird behaviour in the manner he wanted. Even as recently as the 1950s, bird behaviour was seen as a somewhat arcane or difficult–to–do part of ornithology, and certainly not of great interest to amateur naturalists (Marren, 2005:203).[182] Tinbergen gave prominence to the observation of bird behaviour in his popular books, both in the 'how to' sections, and also in the general information sections. In doing so he helped to promote the idea that behavioural studies were both possible and significant.

In Bird Life (1954) Tinbergen gave the impression that the central reason for amateur

182 This point is clearly made by Peter Marren in his history of 'The New Naturalists' books, called, unsurprisingly The New Naturalists. He describes how Tinbergen's The Herring Gull's World (1953b) was extremely unusual in the series for focusing on behaviour, and this caused tension between the series editors including Julian Huxley, and the publishers who were worried it would affect sales: 'The trouble from the publishers' point of view was that The Herring Gull's World did not fit in well with the other books and seemed a better candidate for the university press. It did not pretend to be a complete biology of the herring gull, and in those days animal behaviour was regarded as a specialised and rather arcane field.' (Marren, 2005:203)

birdwatching was a sense of scientific pursuit: 'I shall try to interest you in observing birds and in making discoveries of your own about how they live' (Tinbergen, 1954: 203). This was far from being uncontroversial, and the amateur birdwatching community became profoundly split between those who sought to follow the new 'scientific' approach, which Tinbergen both advocated and represented, and those who saw birdwatching as primarily a hobby for relaxation. Tinbergen's popular science books played a key role in this debate, precisely because amateurs who came to birdwatching through them had encountered this scientific approach as the *only* way to watch birds. The debate between hobbyists and amateur birdwatching scientists was fierce, starting from just prior to the publication of The Herring Gull's World (1953b) and Bird Life (1954), and running for most of the 1950s. Moss (2004) describes the splintering of amateur British ornithology into two 'schools' illustrated by on the one hand Rev P.H.T. Hartly and on the other by Bruce Campbell, both of whom were amateur ornithologists of note,[183] Hartly unable to see past the scientific approach and Campbell always conscious that it was an enjoyable hobby (Moss: 2004:194).

Just how much Tinbergen's own work was the catalyst for this division can be seen from interview material that Moss illustrates his article with, where he talks about the influence of the Tinbergian approach in everyday birdwatching:

> It might be thought that this scientific approach would have little effect on day to day birding. But such was the popularity of the new books on animal behaviour that youngsters did try to follow their elders' example. Growing up in Middlesex, a young birdwatcher named Bruce Coleman took his bike, binoculars and brass telescope to Perry Oaks Sewage Farm on the outskirts of the new airport at Heathrow: 'the sewage farm gave me my first Ruffs, Little and Temmincks Stints, Green and Wood Sandpipers, Greenshanks and Godwits. And in quiet summer months I aspired to be a Niko Tinbergen by watching the "forward threat postures and head

183 Campbell was noted as the author of Finding Nests, (1953) published in the same 'New Naturalists' series as Tinbergen's own Herring Gull's World (1953b). The Rev. Hartley was the noted author of 'Bird Watching and Bird Recording,' (1949) and The Bird Garden (1957).

flagging" of the Black–headed Gull colony. (Moss, 2004:191)

Now to me that reads as real hero–worship, the same kind of thing that I used to feel about playing professional football and eventually getting called up for England when I was a kid, but what it really underlines is just how effective Tinbergen's writing for the general audience was. There was a clear appetite for the amateur pursuit of scientific birdwatching, and a large part of the motivation for it came from Tinbergen's own works. Capturing the imaginations of amateurs, while presumably edifying, may have served one final purpose for Tinbergen, in that it could have helped prepare the ground for those people who could potentially become Tinbergian behaviour researchers. However nowhere does Tinbergen explicitly make the connection between writing for amateurs and the future supply of potential ethologists, so we can only leave this as a likely suggestion, particularly as virtually all ethologists began their interaction with nature as amateurs.

Tinbergen certainly did want to ensure that ethology could continue and was concerned by the trends he was seeing in his students, revealed by Tinbergen's correspondence both with Ernst Mayr and also with W.H. Thorpe, Robert Hinde's head at the Cambridge subdepartment of Behaviour at Madingley. With Mayr, in a letter from November 1953, Tinbergen expressed a concern that his new students were increasingly lacking an "uberblick" or overview, and were rather too focused on quantitative approaches or neurophysiological problems – that their interests were not broad enough.[184] The pattern of his fieldwork demonstrated above shows how Tinbergen's field interests were exceptionally broad, and he wanted to transmit this way of working to a new generation. Mayr replied by blaming the current state of biology teaching in schools,[185] particularly its narrow focus on genes and enzymes. Tinbergen's public works, by bringing behavioural biology to the people, worked to

184 Tinbergen, N. 'Letter to Mayr, E'. 20th November 1953, Ernst Mayr Papers, Harvard University Library. Tinbergen particularly complains that their interests are not broad enough, and they are not interested in the whole field of animal behaviour.

185 Mayr, E. 'Letter to Tinbergen'. 15th December 1953, Ernst Mayr Papers, Harvard University Library. Mayr claims that the main reason that a broad appreciation of natural history was becoming increasingly rare in new students was bad schooling: "The main cause of it in this country is the teaching of biology at the level of what in this country is called the high–school (equals gymnasium in Europe). Most of these high–school biologists do not know one animal from another and teach all about genes and enzymes from books."

circumvent these narrow emphases. By writing for amateur audiences Tinbergen helped to maintain the large lay body of interested amateurs, a group that the Cambridge ethologist W.H. Thorpe in particular worried might slowly become disengaged from science by its creeping professionalisation, by people like Tinbergen and himself.[186] Tinbergen's public writing also gave him the platform to perhaps speak beyond merely the amateur community and on to the wider reading public, and in this respect it gave him the chance to justify his work to them.

Section 2.2 Justifying ethology

One of Tinbergen's most accessible and earliest popular books is Bird Life (1954), a breezily written introduction to the lives of birds, largely aimed at the amateur birdwatching market. Initially Tinbergen focused on the purely aesthetic pleasure that can be derived from watching birds, something that would of course be familiar to the amateur audience, and which, as the book is pitched at a very accessible level, with plenty of illustrations but no tables of results or technical graphs, could well have served as an introduction to birdwatching. This approach is introduced quite clearly:

> Birds are beautiful, and many of us enjoy looking at them. Birds are found in the open air, in beautiful scenery, and some of us become tired of concrete and pavement now and then, and enjoy being in the country. Birds are fellow creatures, and in a way are just as interesting as our fellow men. (Tinbergen, 1954:5)

With the country air and the tweeting of distant larks wafting through his presumably largely urban readers' minds, Tinbergen shifts deftly to introduce the first of many comparisons with humans, something that at its hardest end forms a central

186 Thorpe revealed his concerns in a letter about a book that he was writing that was never published. He wanted to write a brief history of British natural history to enthuse amateurs and to demonstrate that they had and could continue to contribute valuable work to ornithology. "Although the book is light–hearted in approach and in many places quite funny (we hope!) it has a serious theme – namely the place of the amateur naturalist in science. This applies not only to biology… but also to some of the great physicists and chemists who contributed so much to biological advance." Thorpe to Tinbergen, 10th March 1974, W.H. Thorpe Papers.

justification for his researches. A little further along the page Tinbergen moves to introduce the possibility that studying bird behaviour can enhance our understanding of human instincts, and moreover that this is a key reason for birdwatching in the first instance. What makes this quote particularly interesting is that Tinbergen slides easily from introducing the enjoyable hobby of birdwatching to justifying the professional study of bird behaviour. He is still writing to answer the question which titles the page "Why do we watch Birds?"

> But even if by 'use' you mean 'material advantage to mankind', there is much to be said in favour of bird–watching. Professional birdwatchers may be trying to find out why certain birds sometimes increase or decrease in numbers. When they know why, they may be able to tell us how to influence the numbers of animals that are of importance to us, either for good or for harm. An understanding of bird behaviour may even help us to understand our own instinctive behaviour. It is not surprising therefore that there are professional birdwatchers who are being paid for their work. (Tinbergen, 1954:5)

Tinbergen's engagement with the public therefore has served already to capture the imagination of the amateur, or the interest of the lay person, but in addition it has certainly helped to justify spending public money on the enterprise. In notes from a talk he gave at the start of a practical research period in camp Tinbergen addresses the questions that outsiders may have asked him or his students. Tinbergen explains that he certainly enjoys his research, though he emphasises that it can be hard:

> People often ask: what is the use of this? It looks quite enjoyable – but what is the justification of spending public money on this? Well – to be frank – we do enjoy it. Even though not all is fun – it can be quite annoying when a gale rips up your tent, or when you are caught out by a spring tide. And the sound of an alarm clock at 3am can make one feel very miserable.
>
> But Society does need people of our type. Once you have learned how

> to analyse animal behaviour you can be very useful say in a fisheries research station – we need to know how fish react to fishing gear, and how to catch them more economically.
>
> We need an increasing number of behaviour students for the purposes of pest control in agriculture, in forestry and in game management.
>
> Also it is becoming clear that our methods are of interest to students of human behaviour. Psychiatrists are beginning to be interested in our work, and some of our graduates have turned to studies of the behaviour of children.[187]
>
> So this work, which started as a hobby is beginning to bear fruit. (Tinbergen n.d. MS.Eng.d.2387).

Although this speech comes from the field, by its content we can see that it was intended to provide the answers – apologetics – to questions frequently faced by his students and himself. The question "why should you get funding for this hobby" is presumably what this speech was anticipating and sought to provide answers for. It suggested potential economic, psychiatric and child development applications for ethological methods. Tinbergen himself showed little interest in the potential economic applications of ethological observation.[188] However late in life he became profoundly interested in autism in children, both as a problem in itself, and as a potential testing ground in the application of ethological methods to psychiatric cases. He also showed interest in more broadly political and environmental issues, to which he also sought to apply ethological methods.

Tinbergen did address these concerns in his public communications as well as in his talks to students. Indeed similar justificatory passages can be found in many of his popular writings (see Tinbergen, 1953b: 238–239; 1954: 5; 1958: 266–271; 1965: 9–10; 1975: 258–264). This was a theme that he carried across not only in his popular books, but also in his public work in other mediums, for example in a broadcast radio

187 The Tinbergian who began to take an interest in child development was Nick Blurton–Jones whose work took him into the anthropology department at UCLA, but with attendant interests in psychiatry.

188 The only Tinbergian whose work seems to have had the potential to have direct economic benefit was Mike Cullen in his pilchard studies, had they helped in the fisheries research debates in which he participated when he was writing his 1965 paper on pilchard schooling.

series given on 'the Third Programme',[189] on the topic of 'The "courtship" of animals'. He begins by setting out what he imagines to be the standard accusation – that the study of bird behaviour is something of 'a harmless holiday–occupation' (Tinbergen, n.d. iii:8) rather than a useful scientific pursuit. After examining various ways that the study of animal behaviour might be useful to psychiatrists and psychologists – for example in the area of child development and innate behaviour – he signed off:

> …but many professional human psychologists and psychiatrists tell me that our type of analysis is helpful to them. And so, because our work may ultimately contribute a little towards better understanding of ourselves, our prying into the intimate life of birds and fish may give us, apart from enjoyment, some other benefit as well. (Tinbergen, n.d. Iii:9)

Tinbergen was true to his word, and especially towards the end of his life he did apply his methods directly to humans, for psychiatric purposes, but not before he had tried to apply ethological reasoning to understanding humans more broadly. This is the subject I shall investigate in the next section.

Section 3: Science of the People, for the People

Tinbergen was always engaged with the public, and from the very beginning he justified his research on birds and other animals in terms of its potential usefulness for researchers on humans. Recall that in Bird Life (1954:5), a book aimed at amateur ornithologists, Tinbergen put in his introduction that birdwatching could potentially lead to an understanding of human instinctive behaviour. The same was true in the closing pages of The Herring Gull's World, (1953:239–41) where he spelled out the utilitarian reason for birdwatching as being 'the practical value this kind of work will have for human psychology and sociology' (Tinbergen, 1953:241). This underlies his own and also his school's role in applying Tinbergian approaches

189 The script that Tinbergen used is undated, but since it is headed 'Three twenty minute talks for *the Third Programme*' it was probably commissioned and broadcast before 30th September 1967, as after that point *the Third Programme* was relaunched as *BBC Radio Three*.

to the study of humans. In this section I will argue *not* that the Tinbergians always wanted to talk about humans, and all the rest of their work was leading towards this. Rather, I will argue, they *always did* talk about humans, in a similar way to the way that they talked about other animals. However Tinbergen's own writing reflects a more difficult arc to explain. His own interest in humans was clear throughout his career, but it changed quite radically over that period. From the publication of Desmond Morris's The Naked Ape in 1968 onwards, Tinbergen maintained an interest in trying to research humans. At first he sought to study humans as a species – much as Morris had done, but this led to the unsuccessful and unfinished Man: Guinea Pig of Evolution (1974–5 M.s.). After his failure with this book, he returned to a more familiar research mode, employing direct observations and even describing the issued concerned in terms of conflict and drives. That issue was autism in children, which we will look at in the final part of this section

Section 3.1 Humans as a part of the animal world

Humans were always a part of the myriad of animals considered by the Tinbergians, and even by Tinbergen himself in The Study of Instinct (1953: 210). Tinbergen repeatedly made the claim that human behaviour could be understood in the same naturalistic and scientific terms as animal behaviour. And this overt supposition that human and animal behaviour were essentially the same kind of phenomenon was reinforced by an undeclared tendency to look at the two kinds of behaviour in the same way. His observations of both animal and human behaviour were informed by his interest in *social drama*, grounded in an anthropomorphic approach runs across studies on the *natural behaviour* of animals and humans. I will show how even the idea of displacement activities was built on a definition which unavoidably includes social drama, as is shown in Tinbergen's own work, but is also exemplified in Morris's Naked Ape (1968).

Tinbergen, in the last chapter of The Study of Instinct (1953), has some suggestions for how his observations can be applied in the case of humans. The idea that bird behaviour and animal behaviour studies would prove to be useful for humans was a

common theme of his popular science writing, even in 'purely' ornithological books like Bird Life (1954) and The Herring Gull's World (1953). Initially I was startled to find these writings on humans, because I had arrived at an interest in Tinbergen from the direction of the Sociobiology debate of the 1970s and 1980s in which Tinbergen was never more than a bit–part player, and in which Konrad Lorenz with his Nazi connections was gleefully seized upon by Sociobiology's opponents as having been the intellectual forebear of the Sociobiologists, alongside nineteenth century eugenicists like Herbert Spencer (Sociobiology Study Group of Science for the People,1976: 187).

Kruuk in his biography of Tinbergen recognised there were 'already references to the usefulness of ethology in understanding human behaviour' (Kruuk, 2003:252) in Tinbergen's writings as early as The Study of Instinct in 1951. Kruuk claims though, that this was tied into an *increasing* interest in popularising his ethology and in making clear its insights for humanity that grew particularly strongly through the 1960s. I feel this does a disservice to Tinbergen's earlier work, which contains more than just references to the possible utility of the ethological approach for understanding humans. The Study of Instinct records direct observations of human behaviour in the last chapter, and in classic Tinbergian fashion contrasts them with the behaviour of related species. Crucially it also applies the idea of the displacement activity to humans: 'Instinctive behaviour in man has been studied in its various aspects: motor pattern, internal factors (motivation), and external factors (sensory stimuli)' (Tinbergen, 1953:208). To illustrate his case he describes what was his most famous discovery, that of displacement reactions:

> Another phenomenon suggesting an instinctive organization in man basically similar to that found in other animals is displacement activity. Displacement activities are by no means rare in man. They are not so easily recognized as in animals because in man learned patterns, like lighting a cigarette, handling keys or handkerchief, &c., often act as displacement activities. However innate patterns may function as outlets in man too. The general occurrence of scratching behind one's ear in

> conflict situations almost certainly has an innate basis. It is striking how often activities belonging to the instinct of comfort (care of the skin) are shown in conflict situations: in women it mostly takes the form of adjusting non–existing disorder of the coiffure, in the man it consists of handling the beard or moustache, not only in the days when men still had them, but also in this 'clean shaven' era. Further it is striking that displacement scratching can be observed regularly in primates. (Tinbergen, 1953: 210)

Tinbergen's observations here are entirely within the pattern of his observations of other species. The 'Casanova' of Tinbergen's fieldnotes was probably granted more of a social life than the abstract man or woman described here whose most expressive action is to light a cigarette in a moment of tension. Several further points must be observed concerning this passage, however, which do mark it out as different from Tinbergian writing about other animals. Firstly there is no "fieldnote" insertion of observations into the published work: we have only Tinbergen's report of his observations, without any more seemingly authoritative reports of the behaviours. Furthermore, no actual fieldnote record exists of these observations, so we may suppose that they not been given the same level of long–term and detailed observation as his gull work. There is also no reference given for the comparative observations made on primates, something that would be unthinkable were he referring from one gull species to another.

Why did Tinbergen find it so easy to recognise displacement activities in humans? A displacement activity is an action out–of–context, which can only be inferred from the behavioural environment, caused by conflicts between "drives". Tinbergen's fieldnotes, as we saw in chapter one, used anthropomorphic approaches to understand the context of a behaviour, in order that it could be analysed. By inserting himself into the animal's life–world, Tinbergen sees 'social drama' in which each animal can play certain roles all governed by their package of innate drives. This viewing of social drama is what Tinbergen does when he watches either human or animal interactions, and in doing so pronounces on the existence and occurrence of

this or that action as a displacement activity. This perspective helped him to identify the drives underlying a behaviour by inferring from an anthropomorphic "reading" of the context of that behaviour – whether it occurred in a situation of 'attack' or 'defence' for example. When his attention turned to humans, Tinbergen took much the same approach, identifying the context in which a behaviour was performed and inferring the stresses and drives that might be activated. He gives an example taken from the observations of the psychologist Bilz (1941). Bilz noted: 'Still another innate displacement activity in man seems to be the occurrence of sperm ejaculation as a consequence of a blocked escape drive at examinations' (Tinbergen, 1953:210). This observation clearly fits with Tinbergian methods and though a little bizarre only makes sense using much the same approach as was taken with birds. There is a direct inference of "the escape drive" to the situation of examinations. Tinbergen quoted this example approvingly, recognising therefore the validity of the way it must have been obtained. This method is to assess the social drama of a situation and identify which "drives" have been activated. Thus the riches of human life become different from animal life only by degree of complexity.

This is certainly how Desmond Morris, Tinbergen's student (and probably the one who became most famous during Tinbergen's working lifetime) thought. Internationally fame came with his zoological classic The Naked Ape which sold in very large numbers. What made it specifically Tinbergian is that it provides not just an extension of the Tinbergian approach to behaviour, but with it one of the clearest expositions of the idea of a displacement activity. At the heart of Morris's scientific definition, there is reliance upon *social drama*, something that we should have come to expect.

> There has been a great deal of controversy about these displacement activities. It has been argued that there is no objective justification for referring to them as irrelevancies. If an animal feeds, it is hungry, and if it scratches it must itch. It is stressed that it is impossible that a threatening animal is not hungry when it performs so–called displacement feeding activations, or that it is not itching when it scratches. But this is armchair

> criticism, and to anyone who has actually observed and studied aggressive encounters in a wide variety of species, it is patently absurd. The tension and drama of these moments is such that it is ridiculous to suggest that the contestants would break off, even momentarily, to feed for the sake of feeding, or scratch for the sake of scratching, or sleep for the sake of sleeping. (Morris, 1968: 155)

At this point Morris is discussing displacement activities in general and across a range of species. At the heart of his definition, and his defence of it as a useful scientific category, is a reliance on 'the tension and drama of these moments': in other words, *what makes displacement activities make sense as a category* is a view of animal interaction based on the principles of social drama. If they break off for a moment from attacking each other to scratch or pull grass, it remains a part of the social interaction rather than being a series of unrelated behavioural phenomena – it is because their interfering drives are 'telling them' to fight or fly – not because the situation has suddenly stopped and another begun. Morris backs this definition with a series of examples, one of which is appropriately enough from observations of the naked ape:

> When the urge to attack and escape are both strongly activated simultaneously, we exhibit a number of characteristic intention movements and ambivalent posturings. The most familiar of these is the raising of a clenched fist… (Morris, 1968: 160)

With this description Morris has recorded an observation of a social drama, which as far as possible is trying to record the *natural behaviour* of the animals. To describe the natural behaviour of a species, which was the *sine qua non* of the Tinbergians, one cannot write out the *social drama* of their lives, and this was something that always made it likely that ethological methods would be transferred from one social species to another including "the human animal", as Morris (1968) subtitled his book on humans.

The Tinbergians's interest in being useful to mankind in general may also have pushed them toward human studies as being perennially the easiest to justify in terms of "producing useful knowledge". Tinbergen wrote two books directly concerned with human behaviour firstly Man: Guinea Pig of Evolution (unpublished M.S.:1974–5), and secondly Autistic Children (with E.A. Tinbergen, 1983).

Section 3.2 Tinbergen's writing on homo sapiens at the species level

Tinbergen's work both in public and at Oxford showed wide interest in humans something which had always been a feature of his work as we saw in the previous subsection. However partly in response to The Naked Ape he began to consider how he as an ethologist should tackle the subject directly. Firstly we will see evidence of his opinion of The Naked Ape and then look in turn at a public lecture and his book on the subject, Man: Guinea Pig of Evolution.

Tinbergen's view of The Naked Ape is hard to be sure of, as on the one hand he wrote positively about it, as Kruuk demonstrated, but later on his opinion seems to have shifted. Thus The Naked Ape became a stimulus for his own work on humans. Kruuk records Tinbergen's enthusiasm for The Naked Ape in a letter to Desmond Morris held in the private Morris archive:

> I have now read practically the whole of *The Naked Ape*, and as I went on, my pride and admiration grew… both contents and style of communication – absolutely masterful. I really mean it: it is a kind of masterpiece… an approach that is very much the logical continuation of the Lorenz–Tinbergen approaches combined – I really congratulate you – the fools who criticize don't know what they're talking about. (Tinbergen to Morris, 1967 in Kruuk, 2003:245).

Tinbergen then was unstinting in his initial praise, in spite of criticism which Tinbergen's letter shows had already begun. It is from a letter to Morris, and that may

flavour Tinbergen's writing on the subject, but in calling The Naked Ape a logical continuation he is at least showing that he thinks it follows on from both his own research, and more importantly from his own methods. Perhaps curiously Tinbergen claims it not as a continuation of his own work, but that of both Lorenz and himself. Partially that may reflect the fact that Lorenz had previously written on humans (both in his Nazi era, and later in 1966, for instance in On Aggression). It may also be an instance of what Burkhardt described as Tinbergen's almost "pathological modesty" (Burkhardt, 2005:5, quotation marks in original), which in this instance leads him to share the success around ethology, rather than claiming it all for himself, as Morris's original supervisor. Following this early excitement however, either this view of Morris's work changed or Tinbergen revealed publicly doubts that he had not revealed to Morris himself. Indeed only a few months later, in his inaugural lecture as Professor of Animal Behaviour, Tinbergen was considerably more critical, something recognised in his correspondence:

> My only excuse for speaking as I did was that, even though a one hour semipopular talk cannot do the subject justice, Konrad's and Desmond's books had to be supplemented, quickly, by a more critical statement lest "Ethology" were widely identified with what seems to be mere speculation. (Tinbergen, N. letter to Moore, John A. 30th April, 1968.)[190]

Tinbergen by this point therefore was clearly worried by the possible consequences of The Naked Ape. With a year's hindsight he had begun to talk about Morris's methodological shortcomings. The inaugural lecture itself received wide publicity, being reproduced in Science in 1968. Titling his lecture 'On War and Peace in Animals and Man', Tinbergen addressed in particular Konrad Lorenz's popular book On Aggression (1966), which examined aggressive behaviour in humans and animals, and also Desmond Morris's Naked Ape. Partly because of revelations about Lorenz's Nazi links, his book had become profoundly controversial. However Tinbergen's lecture sought to address the specifically scientific aspects of Lorenz's work rather than join the broader political controversy. Tinbergen criticised both

190Niko Tinbergen Papers Special Collections and Western Manuscripts, Bodleian Library. MS.Eng.3127.A48

Lorenz and also Morris for emphasising 'our knowledge rather than our ignorance' (Tinbergen, 1968:1411). Instead he sought to show that, at the time he was speaking, ethological methods *could* be useful in the future, but the research had to be done first:

> As an ethologist, I am going to try to sketch how my science could assist its sister sciences in their attempts, already well on their way, to make a united, broad–fronted, truly biological attack on the problems of behaviour.
> I feel that I can cooperate best by discussing what it is in ethology that could be of use to the other behavioural sciences. What we ethologists do not want, what we consider definitely wrong, is uncritical application of our results to man. Instead, I myself at least feel that it is our method of approach, our rationale, that we can offer, and also a little common sense, and discipline. (Tinbergen, 1968: 1412)

Tinbergen was always concerned with methods, as we have seen throughout this thesis. For this reason, he suggests that it is not the results of ethological research that should be directly applied to mankind, but rather the methods of study. His criticism of both Lorenz and Morris therefore is implicitly that they extrapolated from the results of animal study without due care and attention: he criticised Lorenz and Morris for emphasising their knowledge of humans rather than the lack of observations of man by ethologists. The extract from Tinbergen's lecture on man and animals shows us that he was in principle *in favour* of applying his methods to humans, but he did not feel such research had previously been done with sufficient vigour. The difference between his own rather humble approach to the subject and Lorenz and Morris's can be seen from Morris's introduction. Where Tinbergen urged caution in claiming knowledge of humans, Morris had opened the Naked Ape with bombast declaring:

> I am a zoologist and the naked ape is an animal. He is therefore fair game for my pen and I refuse to ignore him any longer simply because some of

> his behaviour patterns are rather complex and impressive. My excuse is that, in becoming so erudite, Homo sapiens has remained a naked ape nevertheless; in acquiring lofty new motives, he has lost none of the earthly old ones. (Morris, 1968: 9)

Tinbergen may well have agreed with the sentiments of this piece, particularly the refusal to bow in the face of complexity. However Tinbergen's lecture, which was partly in response to Morris's book, emphasised how the methods of ethology could prove useful, rather than suggesting that the ethology of humans was already in a position to generate large quantities of knowledge. Tinbergen's lecture does not present the same certainty as Morris's book. Tinbergen was someone who was profoundly influenced by evolutionary and adaptational thinking and may have been inclined to agree with Morris's suggestion that man had lost none of the 'earthly motives', but in his public lecture he avoided declaring this to be proven fact, as Morris had done.

Tinbergen gave a lecture to undergraduate students on humans in a course on 'Animal Behaviour' in 1972. This shows the extent to which his thinking on humans was a part of his understanding of all animals. The lecture itself is called 'the Cultural Ape', undoubtedly a reference to Morris's Naked Ape, which is mentioned throughout, though it suggests that “extreme Naked Apery” faces difficulties. He does see possible routes past this if ethologists could understand the “pre–cultural” environment of prehistory. The lecture was late in the course, and advocates a continuation of comparative studies:

> Comparative studies have helped in recognising and describing aspects of the adaptedness of each species. Done by comparing relatively constant attributes (first motor patterns, then 'deeper structure' such as specialised learning) and their effects in context of niche of each species.
> Extreme 'Naked Apery' tried to apply this to Man. Obstacle: Man's extreme flexibility – at first glance no species–typical traits, and many of them may be parallel cultural adaptations.

> But we could apply the functional–comparative method if we could know the 'precultural' behaviour and environment of our ancestors of, say, some 2 million years ago. Although this is a historical reconstruction of unique, not repeated change of events, one can arrive at a plausible picture. (Tinbergen, 1972: MS.Eng.)

What we can see from this passage is the idea, however difficult, of extending ethology to incorporate humans. The difficulties are apparent immediately, both to Tinbergen and to us: it is impossible to study human social behaviour from an observational direction which encompasses the whole species, when cultural differences are so apparent and so influential on behaviour. His suggested route out – knowing the "pre–cultural behaviour" implied quite different methods to any previous Tinbergian research, which at least initially, when looking for behavioural homologies, did so to suggest patterns demonstrative of a shared evolutionary history. It is also quite different because it clearly cannot be observed in the same way as the contemporary behaviour of gulls. The emphasis on comparative study, seeing displacement activities in humans for instance, follows easily through from applying it to other animals, but the central aim – studying behaviour 2 million years ago – is radically different.

Tinbergen did try to apply the approach he had suggested to his students in the lecture above. He began by writing Man Guinea Pig of Evolution (1974–5), in which he took in a great deal of archaeological data in an attempt to consider the behaviour or homo sapiens some million years ago. Tinbergen's Man was never published, but he spelled out his intentions quite clearly:

> But however admirable many works of archaeologists, anthropologists, evolutionists, geneticists, ecologists and specialists on human behaviour are, I have never seen a short treatise which sees Man, his origin, his history and his present condition from what I considered a balanced biological point of view. And yet I feel that such an approach is more than

> ever needed. (Tinbergen, 1974–5)[191]

By implication this demonstrates Tinbergen's dissatisfaction with Morris's Naked Ape, but more importantly it also sets out his intention to apply his type of analysis to human behaviour and evolution, because he believes it was "needed". This need emerges from his growing discontent with the political climate of the day, which he believed a properly ethological and evolutionary understanding of human behaviour could help to resolve. Man: Guinea Pig of Evolution was intended to fill this gap, showing how ethological methods could be applied to humanity. Within the book Tinbergen actually spends very little space identifying what humanity's problems were, aside from a reference (Tinbergen, 1974–5: chapter two:14)[192] to Rachel Carson's Silent Spring (1962), a seminal book in the development of the green movement and the reaction against industrial pesticides and herbicides. Tinbergen does not go into any real specificity as to the nature of the political problems that he is observing, stating only that he had 'a sense of unease about the way in which Western Society – in which I include the Sovjet Union – is developing.' (Tinbergen, 1974–5: foreword). But the had remarkable faith that young people could find the solutions to these 'problems', and that these solutions would follow an ethological analysis of the human condition:

> It has been my privilege to have come into contact with numerous young people who seriously want to understand "the human predicament", who want to sort out the pros and contras of the multitude of cultures, who want to find the corn among the chaff, and, most encouragingly of all who want to do something constructive.
>
> My most intensive contacts have been with the students of our newly established course in the Human Sciences at the University of Oxford. This little book summarises the gist of what I felt they ought to know and understand. I make no apologies for having ventured outside my own

191 Unfortunately the individual sections of the manuscript holdings of Man: Guinea Pig of Evolution are undated. In addition rather than being catalogued as a single item they run across a series of consecutive folders from MS.Eng.c.3139/c141 through to MS.Eng.c.3139/c145. The draft of the foreword quoted above is from MS.Eng.c.3139/c141.

192Each chapter of the manuscript is paginated separately, not consecutively.

> field of first–hand research, nor for claiming that I consider my approach to be potentially more helpful than the contributions made by those who are not quite at home in "whole animal biology" – I believe that much of what is being published on our subject suffers from insufficient comprehension of what whole animal biology has to contribute. (Tinbergen, 1974–5: foreword)

Several things come out of this passage – firstly the establishment of a new undergraduate course on 'the Human Sciences' which sought to combine ethological, psychological and social scientific approaches to humans. Tinbergen was instrumental in setting this course up and lobbied hard for its creation (Hinde, 1990: 558; Kruuk, 2003: Ref). This again shows Tinbergen's commitment to studying humans from an ethological perspective. Knowing that Tinbergen had set up a course on the human sciences, the rest of the text makes considerably more sense. His book is clearly intended to address the kinds of questions faced by his students on this course, which he encapsulates in the idea of studying 'the human predicament.' Further down the passage he suggests that although he had strayed far from his area of expertise his approach has more to offer than those not from a "whole animal biology" perspective, which given the make–up of the class was likely to be the social scientists and psychologists.

What is interesting about the book as a whole is the absence of any ethological observation from it. Tinbergen offers no studies of contemporary humans, nor does he show any interest in participating in the archaeological work that he recounts to the public. Perversely then, Morris's The Naked Ape, which Tinbergen had criticised, included more 'ethological research' than did Tinbergen"s own attempt to discuss humanity. Instead, Tinbergen expressed only a Malthusian glumness against the global population growth (Tinbergen 1974–5: chapter 2: 14). His lack of interest in actually applying ethological methods to human is particularly striking. There is no indication of intensive field research, nor any great indication that this research was forthcoming. Instead the book consists largely of uneasy prose and evolutionary history, garnered from secondary sources rather than from his own work.

The book was never finished. There is no indication of the reasons for this failure either in Tinbergen's letters or notes. But we might reasonably surmise that Tinbergen abandoned this project because, fundamentally, it added very little in the way of ethology to the study of humans, and more importantly *it did not apply the field methods* with which Tinbergen had observed his animal subjects of study. Tinbergen remained interested in the wider problems of human life until the very late years of his life, writing with Robert Hinde to The Times on the issue of nuclear disarmament, for example, in 1982 (Hinde, Tinbergen and Spencer, 1982), and trying to persuade Morris to make a television series on 'the predicament of man' (Kruuk, 2003:298). But did not really try to apply ethological methods to explain human behaviour at the species level after the failure to complete Man.

Section 3.3 Tinbergen on the individual human predicament

After the failure of Man, Tinbergen's interest in humans moved to an area where he evidently supposed his previously successful field methods could be more directly applied – the area of autistic children. There were many psychiatric conditions that the Tinbergens (this research was done with his wife Lies) could have applied themselves to, but autism was especially well suited, because its characteristics often include considerable speech difficulties or a total absence of meaningful language–based contact. Moreover, autistic children were very easily upset by outside intervention. This lack of language and potential for being alarmed by observers were characteristics that autistic children shared with Tinbergen's previous animal subjects (Tinbergen, 1983:206; Kruuk, 2003:275).

Kruuk suggests that the Tinbergens' autism work made recommendations which had 'little to do with their ethological study and hypothesis' (Kruuk, 2003: 277). He also chastises the Tinbergens for lacking proper data (ibid.) and lacking objectivity, summing up their work thus: 'Hard science it was not' (ibid.). Seen in the light that I have shed on his fieldnotes, I am not sure that many of Tinbergen's studies would have passed this stern test. Tinbergen's intuitive and frequently anthropomorphic

field approach is the basis for autism work, in effect anthropomorphising autistic children in order to study them. What I mean by this peculiar statement is that just as he had done on his gulls, he set out to understand autistic children by looking at what was of stimulatory significance in their environment, in order to impute what things they might have been reacting to. By doing this, they could then "see" what the emotional and stimulatory context of any behaviour was, just as they had done earlier with wild gulls. The behavioural context could then be used to infer what "drives" might have been activated. This was talking about the world 'as the gulls might say', which I discussed in chapter one. He tried to do the same thing when observing autistic children, studying the context in order to see the drives activated in their (mis)behaviour. As a consequence of comparing his gull work and his work on autistic children, I feel justified in suggesting that the autism studies do fit better with the rest of Tinbergen's opus than Kruuk is comfortable admitting.

The methodology discussed by the Tinbergens was covered in their section 'Some Points of Method' (E.A. & N. Tinbergen, 1983 19–24). In this section the Tinbergens argue that previous studies of autistic children, largely by psychiatrists, ignored the social and environmental context that stimulated them. For example:

> The problem of autism can be understood only if the children are studied in their interactions with their total environment; with their mothers to begin with (with whom they have their first contacts); next with their fathers, their sibs and other children; and, as 'affiliation' with them develops into 'socialisation', with even more persons, with a steadily growing circle of acquaintances. It is just as important to study their interactions (and often their failure to interact) with their non–social environment: with toys, with their own rooms and their own corners; with their own 'comforter'; and with things in the garden, in the street, in shops and in other people's homes, with pets etc.
>
> For all these reasons we have observed children as much as possible in their natural environments, i.e. in their social settings and in the non–social, explorable but not explored world, of which they are the, so sadly

> malfunctioning, centres. Very few psychiatrists do even a minimal amount of such 'fieldwork'. (E.A. & N. Tinbergen, 1983:21)

To me, and I hope to the reader at this point, what the Tinbergens are writing at this point is far from out–of–character with the way that Tinbergen had previously described his methods. His insistence on understanding the stimulatory context, explored in chapters one and two of my thesis, should be familiar. Not only that but his chiding of psychiatrists for their lack of "fieldwork" is strikingly similar to the types of comments he made nearly thirty years before about students who were uninterested in doing fieldwork, or who tried to circumvent the long–term study of their species prior to investigating a particular aspect of it (c.f. Tinbergen, 1953a: 130). The psychiatrists' lack of 'field observation' experience may partly have insulated Tinbergen from their criticisms of him:

> We realise now that the sharp dichotomy in the reaction to our publications could have been predicted. Those in daily contact with autistic children understood us because, much like we field ethologists, they had always studied the children in their home environment. Psychiatrists and psychologists rarely do 'fieldwork'; instead they rely largely on office interviews (often with parents rather than with the child), on questionnaires, and on a variety of 'tests' and their criticisms of our work reflected this methodological bias. So far, they seem not to have understood our procedure at all. Therefore, far from discouraging us even the negative reactions to our first publications rather strengthened us in our resolve to continue on our chosen road, and prompted us at the same time to make a new attempt at explaining to non–ethologists our methods and the conclusions to which had they led us. (E.A. & N. Tinbergen, 1983: 3).[193]

193 Tinbergen had faced stern criticism from psychiatrists, including a ten–page refutation in the journal Psychological Medicine (Wing & Ricks, 1976). The psychologist Schonebaum (1975) argued that Tinbergen's undervalued the importance of genetic factors; the psychologist and child development worker Rimland stated that autism was clearly a 'biochemical abnormality closely related to a unique behavioural syndrome (Rimland, 1975: 402).

Tinbergen's insistence on the value of applying ethological methods to studying autistic children was crucial to his endeavour. Kruuk does not miss the opportunity to declare that such methods were 'not properly applied by the Tinbergens themselves' in this work (Kruuk, 2003: 278). But it is worthwhile to consider their methodological writing which we can find in the Tinbergens work. Once again I feel it stands higher than Kruuk allows:

> Whenever we observed, saw films of, or read accounts of the way autistic children are examined, tested, assessed and taught, we realised that, as animal ethologists with special experience in the study of wild animals in their natural environment, we were particularly aware of the indisputable fact that, like wild animals, autistic children are prime examples of organisms – of functioning systems in general – that are highly sensitive to *'observer interference*'. Like most wild animals, autistic children respond to a stranger primarily by withdrawal, and this reaction is so strong that it suppresses all other behaviour. This is why field ethologists go to such lengths to apply, even more meticulously than good hunters do 'field craft' and 'hide craft'. It is clear to us that the vast majority of researchers, teachers, therapists and even parents of autistic children are unaware of the imperative need for 'making oneself scarce', either by being really concealed or by waiting until one is ignored or at least no longer feared or resented by the child. (It took Dr Iain Douglas–Hamilton and his wife Oria – see their book *Among the elephants* – four years to become accepted even by the less suspicious members of the Lake Manyara National Park in East Africa.) (E.A. & N. Tinbergen, 1983:206)

What strikes me about this extract is how easily it could have been located at any point in Tinbergen's career, or in the life of his school. It concerns natural behaviour; it involves relatively easy contrasting of behaviours across species – nervous elephants and autistic children; and it insists on the value of lengthy observation and

the importance of field craft. In a manner similar to his contrasting of fish with birds, or even with the identification of displacement activities in humans which he had suggested in the Study of Instinct in 1951, Tinbergen continues to seek cross–species comparisons. As a point of method Tinbergen set out to compare conflict behaviour in animals and man (Tinbergen 1983: 35) suggesting dozens of comparisons between various aspects of many animals behaviours and those of humans. For example:

> '*Redirected Movements*'. In a hostile encounter, (territorial or otherwise, e.g. in peck order disputes), one or both of the opponents will make (often violent) attack movements, but they aim them (as we do) at anything *but* their opponent; if a less feared animal is at hand, this will be attacked. Similarly, a man who has been told off at work by his boss is likely to 'take it out' on his secretary or, at home, on his wife and children. (E.A. and N. Tinbergen, 1983:44 italics in original)

In this paragraph the instant switch from animal observation to human anecdote is immediately apparent. The 'redirected movements', a consequence of a drive not fully satisfied by the conclusion of its pattern or mechanism, is made familiar because we understand the human analogue. This quote is an instance of anthropomorphism, as the animal behaviour is made sense of in the light of the vignette about the human man taking his stress out on his secretary or wife. However the vignette occurs in a book about children, and the animal reports were included to make sense of the human behaviours. Thus we find a strange and peculiarly Tinbergian circularity in which animal behaviours are understood through human analogues, even when the point of the study was to make sense of human behaviour in the first place.

Tinbergen's writing about the children he studied is supplied in “case notes” toward the back of Autistic Children. These notes are very similar in style to his writing from his popular science books such as Curious Naturalists (1958). The children appear by name and Tinbergen is happy to write about the circumstances of the observation: both characteristics familiar from Curious Naturalists. For example the

Tinbergens describe their first contact with the girl “Fae”:

> In August 1977, when Fae was 21½ months old, we visited the family for the first time after the parents marriage. We knew nothing of their circumstances but resumed personal contact because we happened to be spending our holiday not far from them. On our arrival we found John asleep in his pram in a sheltered place in the courtyard, and Fae sitting up in her pram in the garden, out of sight of John. The mother, with Adrian nearby, was working in the garden some 70 yards away. Fae, whose toys were lying scattered on the ground around her pram, did not look at us, did not invite contact but neither did she cry; she just stared past us, and repeatedly shook her head in a stereotyped way. When, later, her mother took her from the pram the girl faced away from us or looked past or 'through' us frequently head–shaking. (E.A. and N. Tinbergen, 1983:289)

This account has the level of descriptive detail characteristic of Tinbergian observations. Tinbergen notes the child's movement–by–movement actions, describing how Fae did not look at them but instead shook her head, something that she did once again, this time facing away from them when her mother took her out of the pram. Alongside the movement–by–movement detail Tinbergen records a sense of the location of the observation, both physically and in terms of the stimulatory context of the child. Amongst the things reported are: the distance the mother is from the child; the location of the toys; and the location of the sibling children. All of these notes add up to a very full descriptive picture. This throws light on Tinbergen's own way of being Tinbergian, all of these factors were things that he looked for in his bird and other animal watching. Indeed the description 'head-shaking' is one that is taken directly from his birdwatching and fulfills the classic criteria of being both descriptive and also non-directive as to cause or function. Tinbergen was indeed closer in his own public writing style to the approach that was shown by his student Moynihan than that of Hinde. However his observations remained as intuitive as they had been in the field, of the type that another of his students, Ian Patterson, had directly criticised, as we saw earlier in the thesis.

The Tinbergens' explanations for autism are less fully formed. In the methods section they do talk about conflicting drives being involved, although they use the term 'motivations' (E.A. and N. Tinbergen, 1983:42). They also added a long list of societal and environmental causes to the purely drive–conflict explanation. In 'Fae's case the Tinbergens analysed the causes of her autism:

> The following circumstances seem to us to have been autism–inducing: possibly the forceps delivery; in hospital the mother–child interaction was seriously disrupted in the first few days; the baby had sucking difficulties which were not detected at first; she was switched from (ineffectual) breast–feeding to bottle–feeding and back to breast–feeding; the family had to make a drastic move and had to adjust to new conditions while the parents were under stress of various kinds; the next sib was born only 13 months after her own birth. Her consequent withdrawal elicited a well intentioned but almost certainly harmful withdrawal by the parents (which was intended as an adjustment to the child's needs). Both the retardation and the stereotyped formalisation of the conflict–head–shaking had occurred as secondary, long–term results. (E.A. and N. Tinbergen, 1983:292)

This mixture of maladaptive societal concerns alongside more immediate stimulatory considerations should remind us not only of Tinbergen's earlier animal work, but also of the more recent failure of Man: Guinea Pig of Evolution. The description of 'conflict–head–shaking' in particular recalls the earlier work on drives, and drive conflict, which underlay so much of Tinbergen's work, but most especially underlay Tinbergen's idea of displacement activities. Indeed the Tinbergens extensively discussed displacement activities in both animals and man in Autistic Children (Tinbergen, 1983:41–47). The societal causes he suggests give the idea that the autism could have been due to the medical interventions in the early lives of children, or to a hospital–induced problem in the mother–child bond. This second type of possible cause for autism does chime very strongly with the somewhat anti–society

or at the very least anti–civilisation trend that Kruuk recognised as a feature of the Tinbergens' autism work (e.g. Kruuk, 2003: 277).[194] It is not however directly compatible with the idea that autism emerges from drive conflict, as the Tinbergens suggests in the same quote, because drives were seen to be functions of innate dispositions, whereas the societal worries that the Tinbergens mention as potentially autism inducing were entirely novel in evolutionary terms. That this analysis built on a strange mixture of social and innate causes may not have helped the Tinbergens in their attempts to counteract autism in children. The circularity involved in applying anthropomorphically understood animal observations back to humans may also have played a part in the ultimate failure of the Tinbergens' brief attempt to ally psychiatric practice with that of ethology. Nevertheless Tinbergen's application of his own methods to autistic human children did demonstrate that ethological study of psychiatric conditions in humans, and by implication therefore perhaps all human behaviour too, was possible. It also shows us how Tinbergen himself worked as a Tinbergian, by following his intuitive observations, and writing about them in the same kind of public prose style as he had used to describe birds and other animals over the many years of his career previously.

Conclusions

What have we learned from this rather eccentric and eclectic side of the Tinbergians standard operations? I think the lessons are multifaceted, but before we go into them in detail, one consideration bears repeating: that even ignoring the output of other Tinbergians, like Hans Kruuk's Hyena (1974), or Robert Hinde's popular Why Good is Good (2002), the output of the most famous three Tinbergians – Tinbergen himself, Morris, and Dawkins – adds up to literally hundreds of popular articles and books. By volume, this output must be considered as significant a part of the

194Kruuk is quite dogged in his criticism of Tinbergen's work on autism, and this criticism may explain why this section of his book was rather thin in academic terms, and periodically lacked proper referencing. The following passage therefore is quoted but unreferenced by Kruuk:

> We are damaging the human breeding stock of tomorrow. Quite apart form, for example, the effects of starvation, of lead poisoning etc. on children's brains, we cause by breaking up the social context of groups of extended families and even of family life itself, very serious long–term damage: we breed and raise women and men who have not had the chance to develop fully their potential for optimal parental behaviour. (Kruuk quoting Tinbergen, 2003:277)

Tinbergians work as their academic writing. And as all of the people mentioned in this paragraph (excluding Tinbergen himself) have continued to publish popular works up to the present day, the importance of interacting with the public has to be seen as one of Tinbergen's enduring lessons to his students. –

The second significant finding is to do with the relationship between Tinbergian field practice and popular reporting, an area where I have demonstrated that there was often a surprisingly close link, and one that I have shown was sometimes closer than with the academic writing. I have also discussed why it was that the Tinbergians were so concerned to engage with the public, arguing that it served several purposes. Firstly it allowed him to communicate with the large number of *amateurs* in the field, and to convince them that not only were behavioural studies significant, but also that they were a fundamental part of how animal and specifically bird observation should be done, along with explaining how to do them. Secondly it helped to justify their work as *professionals* on animal behaviour as being useful for humanity, something that was always a concern for Tinbergen (c.f. Kruuk, 2003).

The third significant finding is that the Tinbergians were not only committed to communicating their discoveries to the public, but were specifically interested in showing how their approach and its findings could be useful to the public. This commitment to do science in the public eye was not only unusual, but also what later led them into controversy, particularly when they did indeed attempt to apply their approaches to understanding human behaviour. This was always a stated aim even of purely ornithological work written for amateur audiences, as we saw with Bird Life (1954). That this caused little outrage in the 1950s is perhaps a function of the social climate of that era, relative to the more politicised times of the outcry over The Naked Ape (1967) or Selfish Gene, (1976).

The larger story of this chapter however has been a continuing arc in Tinbergen's work, in which I have shown that Tinbergen's observations on animals, which had always had an anthropomorphic character predisposed him to turn his interests to

questions of humanity. Because he observed and often understood animal behaviour by using anthropomorphism, something evident in the fieldnotes but not in the published work, he was used to trying to understand by imputing motives and by making analogies with humans in similar contexts of social drama. Morris's work, The Naked Ape (1968) prodded Tinbergen into action, and interestingly made use of similar processes – it applied ideas built on anthropomorphic ideas of social drama observed in animals, such as the displacement activity, and reapplied those ideas to humans.

Tinbergen was ambivalent towards The Naked Ape, first praising, and later criticising it. However his responses to it were twofold, firstly to caution against the sense of certainty that Morris's work contained – instead Tinbergen emphasised the lack of ethological knowledge on humans. Secondly he began to write his own version, however his version, Man: Guinea Pig of Evolution partly because it relied on a totally different, and profoundly un–ethological way of research (such as using archaeological material) was never finished. Instead Tinbergen almost went back to methods that had served him well for a lengthy career – observation of living cases and application of relevant data or methods learned through studies on any other species. The result of this later work was Autistic Children (1983), which even included his photographs of gull behaviours (e.g. E.A. and N. Tinbergen, 1983: plates 8–12 between pages 54 and 55) as comparative examples of similar behaviours. Kruuk in particular has treated the work on autism as being something that was not of standard and not of great interest, however I have shown just how comfortably it fits with the body of work from the rest of Tinbergen's career, and with the observation style common to him and his students. It also shows and indication of how Tinbergen's own approach both to observing and writing could be seen as Tinbergian – he was in writing public terms at least close to his student Moynihan, as is shown in his autism writing, but observed in much the same intuitive and anthropomorphic style that we have seen throughout this thesis, but particularly chapter one.

Conclusions

This thesis has investigated the methodology and practice of the Tinbergians, as they developed at the University of Oxford. In particular it has taken in turn Tinbergen, and then some of his more prominent or interesting students, each of which has different ways of interacting with the Tinbergian heritage, and was chosen to illustrate different tendencies and tensions within it. This thesis has shown several themes in Tinbergen's own work, and that of his students, using previously ignored or sidelined material, especially Tinbergen's fieldnotes and his students' D.Phil theses. Historians have tended to focus either on his published work as the basis for their assumptions about his school's practice (as Crist did); or his letters (as Burkhardt so fruitfully has done); or their own personal recollections (as Kruuk partially did). The fieldnotes and the theses therefore have played something of a minor role in the previous historiography.

This thesis sought to change the focus of the research on Tinbergen and his students. In terms of important findings this thesis has principally shown that the published academic or scientific writings of the Tinbergians are a poor guide to understanding what was actually happening in the field. Tinbergen's own published writings on ethological methods and methodology do not agree with the accounts of what happened there as revealed in his fieldnotes. This is not meant as a post-hoc criticism of Tinbergen or any of his students; rather it reveals the gaps between programmatic statements about scientific practice (methods writing and methodologies) and actual field and laboratory work. By looking very intensively at the ways that Tinbergen said he wanted to observe, and seeing too the ways that he actually did so, we have seen the that practice did not necessarily follow principle.

We also saw the effects of unexpected contingencies on Tinbergen's observational practice. In the field these included the common intrusions of other animals, circumstances or people into an uncontrolled space – something that Kucklick and Kohler had noted was a common part of trying to do science in the field. In the field,

for Tinbergen, this was shown in things such as the abrupt change from specific observations of gulls, to general delight at a passing pod of orcas (killer whales), definitely not subjects that were treated as suitable for scientific reportage. In the laboratory, the wildness of the animals led to Morris's unexpected observations of how birds behaved in their winter quarters – observations that proved to be scientifically valuable, and that were published in the scholarly press. In the field, however, much of this type of general surprise and enjoyment is attributable to the *joie de vivre* with which both Tinbergen and his students went about their work, and which they knew to cut from any scholarly writing. We noted that this kind of writing appeared in Tinbergen's fieldnotes, but it also appeared in his writing for the popular press, something that has perhaps been overlooked by Crist, who saw Tinbergen as the arch-mechanomorphist.

The argument chapter by chapter

Crist's work was particularly criticised in chapter one of this thesis. I set out Tinbergen's background, particularly his early amateur interest in birdwatching that pre-dated his scientific work. This was important in refuting the idea that Tinbergen had no feelings towards or affection for the animals he studied. We then followed through to Tinbergen's own writing on method, both that which was published and also that which remained only in the fieldnotes. We identified the aim of fieldwork as being to produce a complete list of the behaviours of a species in order that it could then be used to compare that species' behaviours with those of related species. This was part of the early project of ethology, where it saw itself as a branch of comparative morphology, and in which behaviours were treated as organs similar to those found in a morphological dissection. Tinbergen stated that he sought to observe and describe behaviour in a movement-by-movement fashion and to eschew guessing at function or possible evolutionary origin, and focus only on providing extremely detailed descriptions. This became particularly important when we came to look at the most surprising of Tinbergen's fieldnotes, 'the tale of Casanova' in which, by using the language of anthropomorphism, Tinbergen recorded a wonderful vignette from the social drama of the gulls. Indeed we saw that Tinbergen and his fellow observers were so enraptured by the drama they were witnessing that they

cheered, demonstrating clearly that they were not distant uninterested spectators. This chapter, and indeed this vignette, ably demonstrated a second trend in Tinbergen's fieldnotes, one that is revealing particularly as he was such a public opponent of the use of anthropomorphism as a scientific tool. This vignette, amongst other writing that we investigated, showed that anthropomorphic reading of the behaviours of the animals around him provided him with a crucial way of understanding and describing the features of the world 'as the gulls might say'.

In the second chapter, we moved focus, looking in the first half at Tinbergen's students and his contemporaries, showing how much they had in common, particularly their common heritage as amateurs – an idea mentioned by Röell – and showed how this applied in the case of the Tinbergians. Moynihan's background was investigated from his letters to Ernst Mayr, which frequently included questions about possible training or careers for an amateur ornithologist such as himself. Both Robert Hinde and Aubrey Manning were shown to have roughly similar heritages, also being amateur birdwatchers before they joined Tinbergen. Rather we saw that deriving great pleasure from studying birds was something shared by the Tinbergians and also common to the ethological community at large. In the second half I looked at how the methods and practices of the Tinbergians were applied by two of Tinbergen's early field students, Robert Hinde and Martin Moynihan. Tinbergen's earliest student, Robert Hinde, because he had begun his research prior to Tinbergen’s arrival in Oxford, showed multiple influences in his work, some assuredly Tinbergian, as well as others besides. This contrasted with the next student, Martin Moynihan, who arrived when Tinbergen had fully established himself; Moynihan's work was shown to be exemplary in form and writing for the early school's work, focussing purely on recording the behaviours of gulls movement-by-movement, and including analysis only at the level of direct stimulus and causation. Moynihan's approach also showed another key feature of the early school – a very low level of intervention in the lives of the animals being studied, in his case almost

none at all. Likewise, in the case of Hinde, such intervention was present only at a very minimal level, and only to aid observations made by the naked eye. Both of these students clearly subscribed to the ethos of the early school, which was that natural behaviour should be studied with minimal intervention, and in the field if at all possible.

Where an animal's behaviour could not, for whatever reason, be studied directly in the field, it was brought into the Tinbergian laboratory. In the wider historiography Tinbergen's laboratory has been largely overlooked in favour of his own and some of his student's fieldwork. However I showed that valuable and interesting work was done there, highlighting the behaviour and genetics work. This work, by Margaret Bastock, was certainly not a central part of either Kruuk or Burkhardt's works, and has only been recognised by contemporary biologists – particularly Cobb (2007) and Houck and Drickamer (1996). In terms of the wider story of this thesis, I showed how the laboratory practice of the Tinbergians was inspired by an image of fieldwork, and particularly the movement-by-movement studies of behaviour which we saw in the field as well. We also saw that the object of the Tinbergians' studies became clearer, when it was no longer possible to study it all in the field; they focused on the study of natural behaviour, and above all they valued direct observation. Indeed one study in particular – Mike Cullen's study of pilchards demonstrated that when choosing between indirect observation (via sonar, for example) and direct observation, they chose the latter, even where it risked perverting the behaviour they were studying.

Chapter four looked at both the laboratory and field and how they changed over time. It began by looking at the impact of Esther Cullen's work on kittiwake adaptation, showing how it was a development of the early ethological interest in compiling ethograms, but added a novel focus on evolutionary adaptation to a particular niche. This shifted the direction of ethological fieldwork done by the Tinbergians, something that was reflected in the later theses which I studied: those of Colin Beer, Nick Blurton-Jones and Heather McLannahan. All of these later theses reflect

evolutionary interests, and offer adaptational explanations of behaviour – something that was not present in the early work by Moynihan for example. Tinbergen also worked in this adaptationist vein, studying egg-rolling in chicks with Kruuk amongst others, and writing extensively to publicise Cullen's work to both the popular and academic press. Turning to the laboratory, we saw that there were considerable changes there, as much to do with methods as with explanations. Firstly we saw that birds were studied in cages for the first time, notably by Morris, and subsequently by both Dawkins and Delius. I showed that both Dawkins's and Delius's work revealed considerable drift from the 'field ethos' that had so permeated the early laboratory. Dawkins's work showed little interest, too, in any of the lengthy observational studies that had previously been a staple part of the Tinbergians' projects, instead taking thousands of newly hatched chicks and only performing a single experiment on each. Delius's work moved the Tinbergians into radically new territory, as it involved both vivisection and post-mortem dissection, something which was very different indeed from the early non-interventionist ethos of the school. However there were also strong continuities that ran through the across many of the Tinbergians' work over its entire period, and these were equally apparent in this chapter. The first was a commitment to the study and identification of *natural behaviour*. Dawkins for example, even in his studies which looked so different to those of the purely observational early Tinbergians, was still interested in unravelling innate preferences of the chicks he was studying. Delius was also interested in understanding innate behaviours, and even set out to find the brain centres which corresponded to the hypotheses set out by Tinbergen's early studies. That he did not find them, and that they seemed to indicate a much more complex picture of the brain than Tinbergen had supposed, discouraged Tinbergen; but the fact that Delius had begun the experiment in the first place is a consequence of the powerful hold that Tinbergen's early ideas had over the members of his school. Some of the differences that emerged over time actually highlight the continuities between field and laboratory, particularly the trend away from attempting to compile ethograms, and towards investigation of individual aspects of behaviour. This was seen in both laboratory and field, for example in the work of Beer on egg-rolling and Dawkins on colour preference, neither of which showed an interest in the whole pattern of the species' behaviours. A

similar trend toward intervention in the lives of the animals was also shown in both laboratory and field, beginning with Cullen's egg-switching work, and once again running through to Dawkins and Delius at the extreme end.

Chapter five returned to the more thematic approach of the first chapter, though just as that one had touched on Tinbergen's early methods and practice, so this touched on Tinbergen and his students public work. Investigating the large body of work that was directed towards the public, showing this to be both voluminous, and also important in historical terms. I contrasted the fieldnotes with the academic output, and also with the output for the public audience, and demonstrated that in some ways the field practices were better revealed in the rather looser writing for the public than in that aimed at a scientific audience. I also showed that the fieldnotes and the public writing agreed to a great extent in conveying a sense of the wider life of the Tinbergians – certainly something that would have been beyond the scope of the academic writing. I also considered Tinbergen's motivations in writing for a public or general audience, arguing that his public writing fulfilled a dual purpose of publicising his methods to the substantial and growing amateur ornithological community, which it did with perhaps surprising success, and also in justifying his work to the scientific community and to the public in general, something that seems to have been a grave concern for Tinbergen. This chapter also considered the most controversial aspect of Tinbergian research, that which concerned humans. It showed that Tinbergen had always had some interest in humans, and in applying his methods to humans. It also showed that in some ways his own direct work on humans was stimulated by Desmond Morris's Naked Ape, which Tinbergen quickly came to see as potentially damaging for the discipline of ethology. In response to this he gave lectures both to public and to academic audiences on the potential of ethological research to deliver results for man – though he was more cautious than Morris in his assessment of the present state of ethological knowledge about humans. He then set out to write a book on humans, which culminated in his unfinished work Man: Guinea Pig of Evolution. However as this relied largely on secondary sources, and focused on archaeological evolution, it was perhaps not ideally suited either to his normal writing style or topic, and this may explain its failure. Tinbergen did apply

his more usual methods however to the study of autistic children. Indeed the combination of intuitive observation and austere description that we saw dating back to the very earliest part of his career showed how Tinbergen could find new ways to interact with his way of doing science. This work fitted with his frequent declarations throughout his career that suggested he believed ethological methods could and would prove useful in the study of humans, particularly in psychiatric studies.

Closing argument

This thesis has examined several of the Tinbergians including Tinbergen himself. It has tried to examine the different ways that they interacted with the Tinbergian ideals and ideas of research. In doing this I have not sought to claim that the *raison d'être* of the Tinbergians was to study humans, something that might have been inferred from the structure of this thesis, with the final substantive chapter covering this subject. Instead it was to show that, in spite of frequent declarations to the contrary, the Tinbergians made use of anthropomorphic thinking as a tool of their field studies, often in quite different ways, and their individualities were examined across this thesis. This kind of thinking, using human analogies to understand animal behaviour, predisposed them to think about human problems as well – something that Morris and Tinbergen both did. Indeed, they even applied anthropomorphically derived ideas from animal studies on humans – in effect using understandings of animal behaviours derived from human analogues and social drama to explain human behaviours.

The changing interests and practices of the Tinbergians was also shown in this thesis, from the almost puritanical early phase, in which anything other than stimulus-and-response studies were seen as inferring too much from the data, to the later studies in which evolutionary and adaptationist explanations were *de rigeur*. It also showed the growing interventionism of the members of the school, from very broad observational studies, to very intensive studies of small aspects of a species' behaviour.

Finally this thesis has sought to show the individual Tinbergians it examined as individuals, each with their own research interests, which in the case of some of them (Tinbergen himself, along with Desmond Morris and Mike Cullen) were tracked over a longer period, and which changed over that period. The Tinbergians I chose were selected because they each represented either a different point in one of the themes I have identified or because they represent a transition point in the life and practices of the Tinbergian way of working. Moynihan's total no intervention with his subject of study can be contrasted at the other end of the scale with Delius's surgical interventions, and Dawkins's somewhat xenocidal studies, giving us a strong contrast of practices. Esther Cullen's work on the other hand represents a classic point of transition, and in many ways a catalyst for change in those practices.

Bibliography

Unpublished, Archival and Interview Material

Hinde, R., Interview with author, Cambridge, 16th December 2005.

Mayr, Ernst. 'General Correspondence'. Ernst Mayr Archive, Harvard University Library, Harvard University, Cambridge, Massachusetts. HUG(FP) 74.7.

------. 'Correspondence with Konrad Lorenz and Niko Tinbergen'. Ernst Mayr Archive, Harvard University Library, Harvard University, Cambridge, Massachusetts. HUG(FP) 14.17.

Thorpe, W.H. 'General Correspondence'. W.H. Thorpe Archive, Department of Manuscripts and University Archives, Cambridge University Library.

------. 'Curious Scientists: Lighthearted Memories of Cambridge and Elsewhere,' 1983, W.H. Thorpe Papers, Department of Manuscripts and University Archives, Cambridge University Library.

Tinbergen, N. 'General Correspondence'. Niko Tinbergen Archive, Bodleian Library, Oxford University, Oxford. MS.Eng.c.3125 – MS.Eng.c.3143.c.226

———.'Report on the activities of N Tinbergen as University Lecturer in Animal Behaviour from 1 October 1954 till Christmas 1958', 1959, Niko Tinbergen Papers, Special Collections and Western Manuscripts, Bodleian Library.

———. 'Field notebooks, (8 books)', 1952–1972, Niko Tinbergen Papers, Special Collections and Western Manuscripts, Bodleian Library.

———. 'Notes Scolt Head, April– July 1951,' 1951, Niko Tinbergen Papers, Special Collections and Western Manuscripts, Bodleian Library.

———. 'Blackheaded gulls,' 1951, Niko Tinbergen Papers, Special Collections and Western Manuscripts, Bodleian Library.

———. 'Prelim. Animal Behaviour for Psychologists,' 1961–1965, Niko Tinbergen Papers, Special Collections and Western Manuscripts, Bodleian Library.

———. 'A Practical with a difference: Animal Behaviour Practical,' 1965, Niko

Tinbergen Papers, Special Collections and Western Manuscripts, Bodleian Library.

———. ‘Film Seminars and Extramurals.’ 1969–74, Niko Tinbergen Papers, Special Collections and Western Manuscripts, Bodleian Library.

———. ‘References for Tinbergen’s and Dawkins’s Animal Behaviour Lectures,’ 1970, Niko Tinbergen Papers, Special Collections and Western Manuscripts, Bodleian Library.

———. 'Man – Guinea Pig of Evolution,' 1974–1975, Niko Tinbergen Papers, Special Collections and Western Manuscripts, Bodleian Library.

———. ‘Summary of N. Tinbergen’s views (1982 as seen by himself) on his contribution to the study of behaviour.’ 1982, Niko Tinbergen Papers, Special Collections and Western Manuscripts, Bodleian Library. MS.Eng.c.3125 A.4

———. 'Bird City,' n.d., Niko Tinbergen Papers, Special Collections and Western Manuscripts, Bodleian Library.

———. ‘Extramural 7’, n.d., Niko Tinbergen Papers, Special Collections and Western Manuscripts, Bodleian Library. Ms.Eng.c3132/c35.

———. 'The “courtship” of animals: i. The signalling function of courtship movements.' n.d. Niko Tinbergen Papers, Special Collections and Western Manuscripts, Bodleian Library. MS.Eng.c.3143/c226

———. 'The “courtship” of animals: ii. Fighting and threat as means of spacing out.' n.d. Niko Tinbergen Papers, Special Collections and Western Manuscripts, Bodleian Library. MS.Eng.c.3143/c226

———. 'The “courtship” of animals: iii. An explanatory theory of courtship.' n.d. Niko Tinbergen Papers, Special Collections and Western Manuscripts, Bodleian Library. MS.Eng.c.3143/c226

Bibliography of Published sources

Alexander, H.G. *Seventy Years of Birdwatching*. Berkhamstead: Poser, 1974.

Astley, A. "Number of feathers in Nests of Long–Tailed Tits." *British Birds*, 16 (1923): 252–253.

Baerends G.P. and Baerends van Roon, J.M. "An introduction to the ethology of cichlid fishes." *Behaviour, Supplement,* 1 (1950): 1–242.

Barnes, B. *Interests and the Growth of Knowledge.* London: Routledge & Keegan Paul, 1977.

Baker, N. *The New Amateur Naturalist.* London: Collins, 2004.

Bastock, M. "A Gene Mutation which changes a Behavior Pattern." *Evolution* 10 no.4 (1951): 421–433.

Bastock, M. Morris, D. and Moynihan, M. "Some Comments on conflict and thwarting in animals." *Behaviour*, 6 (1953): 66–84.

Bekoff, M. *Minding Animals: Awareness, Emotions and Heart.* Oxford: Oxford University Press, 2002.

Beer, C.G. "Incubation and Nest–building by the Black–headed Gull." D.Phil. diss., University of Oxford, 1960.

Bent, A.C. *Life Histories of North American Jays, Crows and Titmice*. Washington D.C.: United States National Museums, 1946.

Bilz, R. "Zur Psychophysik des Verlegenheitskratzens Beitrag zur Organismuslehre." *Zentralblatt für Psychotherapie und ihre Grenzgebiete*, 13 (1941): 36–50.

Blurton–Jones, N. "Motivation Studies with Birds: with special reference to Conflict and Thwarting." D.Phil. diss., University of Oxford, 1964.

Bond, M. “Feral and Free,” *New Scientist,* 194 (7th April 2007): 46–7.

Borrello, M. E. “Synthesis and Selection: Wynne Edwards Challenge to David Lack." *Journal of the History of Biology*, 36 (2003): 531–566.

Bolhuis, J.J. “Biography of a Brilliant Birdwatcher.” *Science,* 303 (2004): 1140–1141.

Brigandt, I. “Homology and the Origin of Correspondence.” *Biology and Philosophy,* 17 (2002): 389–407.

Breder, C.M. “Studies on the structure of the fish school.” *Bulletin of the American Museum of Natural History,* 98 (1951): 1–28.

———. “Studies on social grouping in fish schools.” *Bulletin of the American Museum of Natural History,* 117 (1959): 393–482.

Burian, R. “How the choice of Experimental Organism Matters: Reflections on an aspect of Biological Practice.” *Journal of the History of Biology,* 26 no.2 (1993): 351–367.

Burian, R. and Lederman, M. “Introduction.” *Journal of the History of Biology,* 26 no.2 (1993): 235–237.

Burkhardt Jr., R.W. “Charles Otis Whitman, Wallace Craig and the Biological Study of Behaviour in America, 1898–1924.” in *The American Development of Biology,* edited by R. Rainger, K.R. Benson and J. Maienschein. Philadelphia: University of Pennsylvania Press, 1983a.

———. “Darwin on Animal Behaviour.” in *The Darwinian Heritage,* edited by D. Kohn. Princeton N.J.: Princeton University Press, 1983b.

———. “The Development of an Evolutionary Ethology.” in *Evolution from Molecules to Men,* edited by D.S. Bendell. Cambridge: Cambridge University Press, 1983c.

———. "The Journal of Animal Behaviour and the early history of Animal Behaviour Studies in America." *Journal of Comparative Psychology,* 101 (1990a): 223–230.

———. "The Founders of Ethology and the Problem of Animal Subjective Experience." in *Animal Consciousness and Animal Ethics,* edited by Dol et al. Assen: Van Gorcom, 1990b.

———. "Oskar August Heinroth." in *Dictionary of Scientific Biography,* vol. 17, 1990c.

———. "Karl von Frisch." in *Dictionary of Scientific Biography,* vol. 17, 1990d.

———. "Ethology, Natural History, the Life Sciences, and the Problem of Place." *Journal of the History of Biology*, 32 (1999): 489–502.

———. *Patterns of Behaviour*. Chicago: Chicago University Press, 2005.

———. "Niko Tinbergen: The Ethologist as Field Naturalist." *Biological Theory*, 2 no.1 (2007): 87–90.

Buss, D.M. et al. "Adaptations, Exaptations, and Spandrels." *American Psychologist*, 53 no.5 (1998): 533–548.

Carson, R. *Silent spring.* Boston, Massachusetts: Houghton Mifflin, 1962.

Campbell, B. *Finding Nests*. London: Collins, 1953.

Cenami–Spada, E. "Amorphism, Mechanomorphism and Anthropomorphism." In *Anthropomorphism, Anecdotes and Animals,* edited by R.W. Mitchell, N.S. Thompson and H.L. Miles. New York: State University of New York Press, 1997.

Clarke, A. *Disciplining Reproduction: modernity, American Life Science, and "the problems of sex."* Berkeley, California: University of California Press, 1998.

Cobb, M. "A gene mutation which changed animal behaviour: Margaret Bastock and

the *yellow* fly." *Animal Behaviour*, 74 no. 2 (2007): 163–169.

Crist, E., "Naturalists' Portrayals of Animal Life: Engaging the Verstehen Approach." *Social Studies of Science*. 26 (1996): 799–838.

———. "The Ethological Constitution of animals as Natural Objects: The Technical Writings of Konrad Lorenz and Nikolaas Tinbergen." *Biology and Philosophy*, 13 (1998): 61–102.

————. *Images of Animals: Anthropomorphism and the Animal Mind.* Philadelphia: Temple University Press, 1999.

Cronholm, B. "Nobel Prize in Physiology or Medicine 1973 Presentation Speech." in *Nobel Lectures, Physiology or Medicine 1971–1980*, edited by J. Lindsten. Singapore: World Scientific Press, 1992.

Cullen, E. "Adaptations in the Kittiwake to Cliff Nesting." *Ibis*, 99 (1957): 275–302.

Cullen, J.M. "A Study of the behaviour of the Arctic Tern (Sterna macrura)*"* D.Phil. diss., University of Oxford, 1956.

———. et al. "Methods for Measuring the Three–Dimensional Structures of Fish Schools*." Animal Behaviour,* 13 (1965): 534–543.

Cushing, D.H. and Harden–Jones, F.R. "Why do Fish School." *Nature*, 218 (1968): 918–920.

Danchin, E. and Nelson, J.B. "Behavioral Adaptations to Cliff Nesting in the Kittiwake (*Rissa tridactyla*): Convergences with the Gannet (*Sula bassana*) and the Black Noddy (*Anous tenuirostris*)." *Colonial Waterbirds,* 14 no. 2 (1991): 103–107.

Darwin, C. *The Expression of Emotions in Man and Animal*. London: John Murray, 1872.

Dawkins, M.S. Halliday T.S. And Dawkins, R. *The Tinbergen Legacy*. London: Chapman and Hall, 1991.

Dawkins, R. "Selective Pecking in the Domestic Chick." D.Phil. diss., University of Oxford, 1966.

———. *The Selfish Gene*. Oxford: Oxford University Press, 1976.

Dehue, T. review of *De wereld von instinct* by D.R. Röell, *Isis,* 88 no. 2 (1997): 356–357.

Delius, J.D. "Das Verhalten der Feldlerche." Ph.D. diss., Georg August Universität zu Göttingen, 1961.

———. "Pentobarbital anaesthesia in the herring and lesser black–backed gull." *The Journal of Small Animal Practice,* 7 (1966a): 605–609.

———. "Some techniques for the electrical brain stimulation of small unrestrained animals." *Medical and Biological Engineering*, 4 (1966b): 393–397.

———. "A Stochastic Analysis of The Maintenance Behaviour of Skylarks' Behaviour." *Behaviour,* 33 no. 1 (1969): 137–177.

———. "Neural Substrates of Vocalizations in Gulls and Pigeons." *Experimental Brain Research,* 12 (1971): 64–80.

———. "Agonistic behaviour of juvenile gulls, a neuroethological study." *Animal Behaviour,* 21 no. 2 (1973): 236–246.

Deichmann, U. *Biologists Under Hitler*. trans. T. Dunlap. Cambridge, Massachusetts and London: Harvard University Press, 1996.

Dewsbury, D. *Studying Animal Behaviour: Autobiographies of the Founders.* Chicago and London: Chicago University Press, 1989.

———. "Rhetorical Strategies in the Presentation of Ethology and Comparative Psychology in Magazines after World War II." *Science in Context,* 10 no.2 (1997): 367–386.

———. "The proximate and the ultimate: past, present and future." *Behavioural Processes*, 46 (1999): 189–199.

———. "Book Review: Patterns of Behavior." *British Journal for the History of Science,* 40 (2007): 147–149.

Durant, J. "Innate Character in animals and man: A perspective on the origins of Ethology." in *Biology Medicine and Society*, edited by C. Webster. Cambridge: Cambridge University Press, 1981.

———. "Exploring the Roots of Sociobiology." *British Journal for the History of Science*, 13 (1980): 55–60.

———. "The Making of Ethology: The Association for the Study of Animal Behaviour, 1936– 1986." *Animal Behaviour*, 34 (1986): 1601–1616.

Ewer, R.F. *The Ethology of Mammals.* New York: Plenum Press, 1968.

———. *The Carnivores*. Ithaca, New York.: Cornell University Press, 1973.

Fabre, J.H. *The hunting wasps*. New York: Dodd, Mead and Company, 1915.

Fatio, V. and Studer T. *Catalogue des Oiseaux de la Suisse*. Geneva: Georg & Cie, 1889.

Fisher, J. *Watching Birds.* Harmondsworth: Penguin, 1940.

———. "The Development of The British Trust for Ornithology" *19th Annual Report of the British Trust for Ornithology*. British Trust for Ornithology, 1953.

Forbush, E.H. *Birds of Massachusetts and other New England states*. Boston, Massachusetts: Massachusetts Department of Agriculture, 1929.

Gieryn T.F. "Boundary–Work and the Demarcation of Science from Non–Science: Strains and Interests in Professional Ideologies of Scientists." *American Sociological Review*, 48 no.6 (1983): 781–795.

Geison, G.L. "Research Schools and New Directions in the Historiography of Science." *Osiris* , vol. 8, no. 1 (1993): 226.

———. *Michael Foster and the Cambridge School of Physiology: The Scientific Enterprise in Late Victorian Society.* Princeton N.J.: Princeton University Press, 1978.

Griffiths, P. "Function, Homology and Character Individuation." *Philosophy of Science,* 73 (2006): 1–25.

Hartley, Rev. P.H.T. *Bird Watching and Bird Recording*. Royal Society for the Protection of Birds Occasional Publications, no. 7, 1949.

———. *The Bird Garden.* London: Royal Society for the Protection of Birds, 1957.

Hess, E.A. 'The Wild Goose Chase." in *Studying Animal Behaviour: Autobiographies of the Founders,* edited by D.A. Dewsbury, Chicago and London: Chicago University Press, 1985.

Hinde, R.A. "A Comparative Behaviour study of the Paridae." D.Phil. diss., University of Oxford, 1951.

———. "The Behaviour of the Great Tit, *Parus Major* and some related species." *Behaviour Supplement,* 2 (1952): 1–201.

———. "The conflict between drives in the courtship and copulation of the Chaffinch." *Behaviour*, 5 (1953): 1–31.

———. "Ethological Models and the Concept of 'Drive'." *The British Journal for the Philosophy of Science*, 6 no. 24 (1956): 321–331.

———. "Ethology in Relation to Other Disciplines." in *Studying Animal Behaviour: Autobiographies of the Founders,* edited by D.A. Dewsbury, Chicago and London: Chicago University Press, 1985.

———. "Nikolaas Tinbergen. 15 April 1907–21 December 1988." *Biographical Memoirs of Fellows of the Royal Society*, 36 (1990): 548–565.

———.*Why good is good*. London: Routledge, 2002.

Hinde, R.A. Tinbergen, N. & Spencer. K. "letter to the editor." *The Times,* November 3rd 1982.

Hibbert–Ware, A. "Behaviour of Titmice under Artificial Conditions." *British Birds*, 23 (1929): 34–35.

Hooper, J. *Of Moths and Men: Intrigue Tragedy and the Peppered Moth*. London: Fourth Estate Publishers, 2002.

Houck, L.D. and Drickamer, L.C. ed. *Foundations of Animal Behavior with Commentaries*. Chicago: University of Chicago Press, 1996.

Huntingford, F.E. "Anniversary Essay: A history of *Animal Behaviour* by a partial, ignorant, and prejudiced ethologist." *Animal Behaviour*, 65 (2003): 1–7.

Hynes, H.B.N. "The Food of Fresh–Water Sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a Review of Methods Used in Studies of the Food of Fishes." *The Journal of Animal Ecology,* 19 no. 1 (1950): 36–58.

Hynes, H.B.N. and Jones, J.W. "The Age and Growth of *Gasterosteus aculeatus*, *Pygosteus pungitius* and *Spinachia vulgaris*, as Shown by their Otoliths." *The Journal of Animal Ecology*, 19 no. 1 (1950): 59–73.

Kennedy, J.S. *The New Anthropomorphism*. Cambridge: Cambridge University Press, 1992.

Kingsley Noble G. and Aronson L.R. "The Sexual Behavior of Anura 1. The Normal Mating Pattern of Rana Pipiens." *Bulletin of the American Museum of Natural History*, 80 no.5 (1942): 127–142.

Kirkman, F.B. *Bird Behaviour*. London: T.E. Nelson & Sons, 1937.

Klopfer, P.H. "Konrad Lorenz and the National Socialists: on the politics of Ethology." *International Journal of Comparative Psychology*, 7 (1994): 202–208.

———. *Politics and people in ethology: personal reflections on the study of animal behavior*. Lewisburg: Bucknell University Press, 1999.

Kohn, Marek. *A Reason for Everything: Natural Selection and the English Imagination*. London: Faber and Faber, 2004.

Kohler, R.E. "Drosophila: A life in the Laboratory." *Journal of the History of Biology*, 26 no.2 (1993): 281–310.

———. *Landscapes and Labscapes: Exploring the Lab–Field Border in Biology*. London and Chicago: University of Chicago Press, 2002a.

———. "Place and Practice in Field Biology." *History of Science*, 40 (2002b): 189–210.

———. "Labscapes: Naturalizing the Lab." *History of Science*, 40 (2002c): 473–501.

———. *All Creatures: Naturalists, Collectors and Biodiversity, 1850–1950*. Princeton and Oxford: Princeton University Press, 2006

Kucklick, H. and Kohler, R.E. "Science in the Field." *Osiris*. 2nd Ser. 11, (1996): 1–14.

Kruuk, Hans. "Predators and anti–predator behaviour of the Black–headed Gull (*Larus argentatus*)." *Behaviour Supplement,* 11 (1964): 1–129.

———. *The Hyena.* Oxford: Oxford University Press, 1975.

———. *Niko's Nature: A Life of Niko Tinbergen and his science of animal behaviour*. Oxford: Oxford University Press, 2003.

Krebs, J. & Dawkins, R. "Obituary: John Michael (Mike) Cullen, (1927–2001)." *Ibis* 143 (2001): 704–705.

Langworthy Fuller, J. "Of Dogs, Mice, People and Me." in *Studying Animal Behaviour: Autobiographies of the Founders,* edited by D.A. Dewsbury, Chicago and London: Chicago University Press, 1985.

Latour, B. "Give Me a Laboratory and I Will Raise the World." in *The Science Studies Reader*, edited by M. Biagioli, New York and London: Routledge, 1999.

Leach, E. "Writing Anthropology." *American Ethnologist*, 16 no. 1 (1989): 137–141.

Lehrman, D.S. "A Critique of Konrad Lorenz's theory of instinctive behaviour." *Quarterly Review of Biology,* 28 (1953): 337–363.

Lewis, E.B. "Alfred Henry Sturtevant." *National Academy of Sciences Biographical Memoirs*. 73 (1976): 2–16.

Lewis, T. "Coal Tit Hiding Beech–nuts." *British Birds*, 16 (1923): 216–217.

Lissmann, H.W. "Proprioceptors." in J. F. Danielli and R. Brown. *Symposia of the the Society for Experimental Biology Number IV: Physiological Mechanisms in Animals Behaviour.* Cambridge: Cambridge University Press, 1950.

Lorenz, K. "Der Kumpan in der Umwelt des Vogels." *Journal für Ornithologie*, 83 (1935): 137–213.

———. "Der Kumpan in der Umwelt des Vogels." *Journal für Ornithologie*, 83 (1935): 289–413.

———. "The Companion in the bird's world." *Auk*, 54 (1937): 245–273.

———. "The Comparative Method in Studying Innate Behaviour Patterns." *Symposia of the Society for Experimental Biology: Physiological Mechanisms in Animal Behaviour,* 4 (1950): 221–268.

———. *On Aggression.* London: Methuen, 1966.

Lynch, M. “Discipline and the Material Form of Images: An Analysis of Scientific Visibility.” *Social Studies of Science,* 15 (1985): 37–66.

———. “The externalised retina: Selection and mathematization in the visual documentation of objects in the life sciences.” *Human Studies*, 11 (1988): 201–234.

Lynch, M. & Law, J. “Pictures, Texts and Objects: The Literary Language Game of Bird–watching.” in, M. Biagioli, ed. *The Science Studies Reader,* New York and London: Routledge, 1999.

Lynch, M. and Woolgar, S. “Sociological orientations to representational practice in science.” *Human Studies*, 11 (1988): 99–116.

Manning, A. “The Ontogeny of an Ethologist.” in *Studying Animal Behaviour: Autobiographies of the Founders,* edited by D.A. Dewsbury, Chicago and London: Chicago University Press, 1985.

Marler, P. “Behaviour of the chaffinch *Fringilla coelebs*.” *Behaviour Supplement*, 5 (1956): 1–184.

Marren, P. *The New Naturalists: Half a Century of British Natural History.* 2nd ed. London: HarperCollins, 2005.

Mayr, E. “Genetic Environment and Evolution.” in J. Huxley, A. Hardy and E.B. Ford, *Evolution as a Process*, London: George Allen and Unwin, 1954.

McLannahan, H.M.C. “Studies of Behaviour Ontogeny in Gulls” D.Phil. diss., University of Oxford, 1970.

———. “Some aspects of the ontogeny of cliff–nesting behaviour in the Kittiwake *Rissa tridactyla* and the Herring Gull *Larus argentatus*.” *Behaviour*, 44 (1973): 36–88.

Mitchell, R. W. Thompson, N.S. and Miles, H.L. eds. *Anthropomorphism, Anecdotes and Animals*. New York: State University of New York Press, 1997.

Morely, A. "Effects of Baiting on the Marsh Tit." *British Birds*, 35 (1942): 261–266.

Morrell, J.B., "The Chemist Breeders: The Research Schools of Liebig and Thomas Thomson." *Ambix*. 19 no.1 (1972): 1-46.

———. "W. H. Perkin, Jr., at Manchester and Oxford: From Irwell to Isis." *Osiris* 8, no. 1 (1993): 104

Morris, Desmond. "Homosexuality in the Ten–Spined Stickleback." *Behaviour*, 4 (1951): 233–261.

———. "The Reproductive Behaviour of the Zebra Finch (*Poephila Guttata*) with Special Reference to Pseudofemale Behaviour and Displacement Activities." *Behaviour*, 6 (1954): 271–322.

———. "The Feather Postures of Birds and the Problem of the Origin of Social Signals." *Behaviour*, 9 (1956): 75–113.

———. "The Reproductive Behaviour of the Ten–Spined Stickleback (*Pygosteus Pungitius*)." *Behaviour Supplement,* 6 (1958): 1–154.

———. *The Naked Ape*. London: Corgi Books, 1968.

———. *Animal Days*. London: Jonathan Cape Ltd, 1979.

———. *Watching: Encounters with Humans and other animals*. London: Max Press, 2006.

Morse Nice, M. "The Role of Territory in Bird Life." *American Midland Naturalist*, 26 no. 3 (1941): 441–487.

Moss, S. *A Bird in the Bush: A Social History of Birdwatching*. London: Aurum Press, 2004.

Moynihan, M. "Some Displacement Activities of the Black–headed gull 1." *Behaviour,* 5 (1953): 58–80.

———. “Some Displacement Activities of the Black–headed gull 2.” *Behaviour,* 5 (1953): 289–304.

———. “Some aspects of the reproductive behaviour of the Black–headed gull and related species.” D.Phil. diss., University of Oxford, 1954

———. “Notes on the behavior of some north American gulls I. Aerial hostile behavior.” *Behaviour,* 10 (1954): 126–178.

———. “Some Aspects of Reproductive Behavior in the Black–headed Gull (*Larus ridibundus ridibundus*) and related species.” *Behaviour Supplement,* 4 (1955): 1–201.

———. “Notes on the behavior of some north American gulls II. Non–aerial hostile behavior of adults.” *Behaviour,* 12 (1956): 95–182.

———. “Notes on the behavior of some north American gulls III. Pairing behavior.” *Behaviour,* 13 (1957): 113–130.

———. “Some aspects of the Reproductive Behaviour in the Black–headed Gull (*Larus ridibundus ridibundus*) and Related Species.” *British Journal of Animal Behaviour*, 5 (1957): 39.

———. “Notes on the behavior of some north American gulls IV. The Ontogeny of Hostile Behavior and Display Patterns.” *Behaviour,* 14 (1958): 214–239.

Newton, I. “Vero Copner Wynne–Edwards, C. B. E.. 4 July 1906–5 January 1997.” *Biographical Memoirs of Fellows of the Royal Society*, 44 (1998): 472–484.

Nicholson, E.M. *The Art of Birdwatching: A practical guide to field observation*. London: H.F. & G. Witherby, 1931.

Nielson E.T. “The Method of Ethology.” *Proceedings of the 10th International Conference of Entomologists,* 2 (1958): 563–565.

North, F.J. Campbell, B. & Scott, R. *Snowdonia*. London: Collins, 1949.

Owen, J.H. “Unusual Feeding Behaviours of Tits.”’ *British Birds*, 38 (1945): 173.

Parr, A.E. "A contribution to the theoretical analysis of schooling behaviour of fishes." *Papers of Bingham Oceanographic Collection,* 1 (1927): 1–32.

Parsons, T. *Essays in Sociological Theory*. London: Collier–Macmillan, 1954.

Pollard, E. Hooper, M.D. & Moore, N.W. *Hedges*. London: Collins, 1974.

Quine, W.V.O. *From a Logical Point of View.* 2nd ed. Cambridge Massachusetts: Harvard University Press, 1964.

Radcliffe–Brown, A.R. *Structure and Function in Primitive Society: essays and addresses*. London: Cohen & West, 1952.

Radick, G. ''Essay Review: The Ethologist's World.'' *Journal of the History of Biology*, 40 no.3 (2007): 565-575.

Reilly, S. "The ontogeny of aquatic feeding behavior in Salamandra salamandra: stereotypy and isometry in feeding kinematics." *The Journal of Experimental Biology*, 198 (1995): 701–708.

Richards, R.J. "The Innate and the Learned: The Evolution of Konrad Lorenz's Theory of Instinct." *Philosophy of Social Science*, 4 (1974): 111–133.

Richards, T.J. "Concealment of food by Nuthatch, Coal–Tit and Marsh–Tit". *British Birds*, 42 (1949): 360–361.

Rimland, B. "Autism, Stress and Ethology." *Science, New Series.*188 no. 4187 (1975): 401–402.

Röell, D.R. *The World of Instinct: Niko Tinbergen and the Rise of Ethology in the Netherlands (1920–1950)*. Assen: Van Gorcum & Co. 2000.

Russell, E.S. *The Study of Living Things: Prolegomena to a Functional Biology*. London: Methuen and company, 1924.

Salomonsen, F. "Tretaaet Maage (*Rissa tridactyla* (L.)) som Ynglefugi I Danmark."' *Dansk Ornitologisk Forenings Tidsskrift,* 35 (1941): 159–179.

Segerstråle, U. *Defenders of the truth: the Sociobiology Debate*. Oxford: Oxford University Press, 2000.

Selous, E. *Realities of Bird Life: Being Extracts from the Diaries of a Life–loving Naturalist*. London: Constable Publishers, 1927.

Sevenster, P. "A causal study of displacement activity (fanning in *Gasterosteus aculeatus*)." *Behaviour Supplement,* 9 (1961): 1–170.

Schonebaum, R.M. "letter to the editor." *Science, New Series*, 188 no. 4187 (1975): 402–403.

Southern, J.B. "Unusual Feeding Behaviour of Tits." *British Birds*, 39 (1946): 214.

Spencer, J. "Anthropology as a Kind of Writing." *Man*, *New Series*, 24 no. 1 (1989): 145–164.

Spieth H.T. "Mating behavior and sexual isolation in the *Drosophila virilis* species group." *Behaviour,* 3 (1951): 105–145.

Sturtevant, A. "The North American species of Drosophila." *Carnegie Institute of Washington Publications,* 301: (1921) 1–150.

Summerhayes, V.S. *Wild Orchids of Britain*. London: Collins, 1968.

Teel, K. Webb, W.B. "Response evocation on satiated trials in the T–maze." *Journal*

of Experimental Psychology, 41 no. 2 (1951): 148–152.

Thorpe, W.H. "The Concepts of Learning and their Relation to those of Instinct." in J. F. Danielli and R. Brown. *Symposia of the the Society for Experimental Biology Number IV: Physiological Mechanisms in Animals Behaviour,* Cambridge: Cambridge University Press, 1950.

———. "David Lambert Lack. 1910-1973." *Biographical Memoirs of Fellows of the Royal Society*, 20 (1974): 271-293.

———. *The Origins and Rise of Ethology.* London: Heinemann Educational Books, 1979.

Tinbergen, N. "On the analysis of social organization among vertebrates, with special reference to birds." *American Midland Naturalist.* 21 (1939): 210–34.

———. "An objectivistic study of the innate behaviour of animals." *Bibliotheca Biotheoretica D,* 1 (1942): 39–98.

———. *Inleiding tot de diersociology*. Gorinchem: Noorduijn, 1946.

———. "De functie van de rode vlek op de snavel van de zilvermeeuw (*Larus argentatus*)." Bijdragen tot de dierkunde. 28 (1949): 453–465.

———. "The Hierarchical Organization of Nervous Mechanisms Underlying Instinctive Behaviour." in J. F. Danielli and R. Brown. *Symposia of the Society for Experimental Biology: Physiological Mechanisms in Animal Behaviour,* 4 (1950): 305–312.

———. *The Study of Instinct*. London: Oxford University Press, 1951.

———. "Derived' activities: their causation, biological significance, origin and emancipation during evolution." *Quarterly review of Biology*, 27 (1952): 1–32.

———. *Social Behaviour in Animals*. London: Methuen & Co., 1953a.

———. *The Herring Gull's World*. London: Collins, 1953b.

———. *Bird Life.* London: Oxford University Press, 1954a.

———. "Courtship and Threat Display." in J. Huxley, A. Hardy and E.B. Ford. *Evolution as a Process*, London: George Allen and Unwin, 1954b.

———. "Appendix II: Autobiographical Sketches of the Participants, Niko Tinbergen." in B. Schaffner. *Group Processes: Transactions of the First Conference*.

New York: Josiah Macy Jr. Foundation, 1955.

———. *Curious Naturalists*. London: Country Life, 1958.

———. "Comparative Studies of the Behaviour or Gulls (Laridae): A Progress Report." *Behaviour*, 15 (1959): 1–70.

———. "On Aims and Methods of Ethology." *Zeitschrift für Tierpsychologie*, 20 (1963): 410–433.

———. "On War and Peace in Animals and Man." *Science*, 160 (1968): 1411–1418.

———. *The Animal in its World: Explorations of an Ethologist 1932–1972: Volume One, Field Studies*. Cambridge Massachusetts: Harvard University Press, 1972.

———. *The Animal in its World: Explorations of an Ethologist 1932–1972: Volume Two, Laboratory Experiments and General Studies*. Cambridge Massachusetts: Harvard University Press, 1973.

———. *Curious Naturalists,* Revised Edition. Harmondsworth: Penguin Education, 1974.

———. "Watching and Wondering." in *Studying Animal Behaviour: Autobiographies of the Founders,* edited by D.A. Dewsbury, Chicago and London: Chicago University Press, 1985.

Tinbergen, N. et al, "Egg Shell Removal by the Black–headed Gull, *Larus Ridibundus L.*; A Behaviour Component of Camouflage." *Behaviour*, 19 (1962): 74–117.

Tinbergen, N. Vowles, D. and Delius, J.D. "Brain Stem Stimulation and Ethological Studies on Birds." *Final scientific rept., 1 Mar 66–31 Feb 67* DTIC number: AD0652507 (1967).

Tinbergen, N. and Tinbergen, E.A. *Autistic' children: new hope for a cure.* London: George Allen and Unwin, 1983.

Waters, M. and Coulson, J. *A Concise History of Ornithology.* London: A & C Black Publishers, 2003.

Weidmann, R. "The Social Behaviour of the Black–headed gull with special reference to food–begging behaviour." D.Phil. diss., University of Oxford, 1956.

White, G. *The Natural History of Selbourne*. Edited and with an introduction by J. Fisher. London: Cresset Press, 1947.

Wing, L. and Ricks, D.M. "The aetiology of childhood autism: a criticism of the Tinbergens ethological theory." *Psychological Medicine*, 6 (1976): 533–543.

Wynne–Edwards, V.C. "The Control of Population Density Through Social Behaviour: A Hypothesis." *Ibis,* 101 (1959): 436–441.

———. "Backstage and Upstage with "Animal Dispersion." in *Studying Animal Behaviour: Autobiographies of the Founders,* edited by D.A. Dewsbury, Chicago and London: Chicago University Press, 1985.

van Wyhe, J. "Review of *A Reason for Everything: Natural Selection and the English Imagination"* by Marek Kohn. *Human Nature Review*. 5 (2005): 1-4.

Appendix A: Tinbergen's Students studied in the thesis

Tinbergen's students were large in number, and this appendix gives a detailed list of the student's whose work I have examined in this thesis, and is to be read as a companion to the next appendix which lists all of the students that I could get certain dates and thesis titles for. In this appendix I will be taking a chapter by chapter approach outlining each of the students studied in the chapter. Chapter one is principally about Tinbergen himself, so I begin with chapter two:

Chapter Two

In this chapter I examined the work of two of Tinbergen's earliest fieldworking students, **Robert Hinde** and **Martin Moynihan**.

Hinde was the earliest of all of Tinbergen's students as he began his work before Tinbergen's arrival in Oxford, as was evident in the mixture of influences evident in his thesis. He arrived in 1949 and had written up by 1951, using a special dispensation due to his time in national service. Hinde studied the Great Tit, *Parus Major* in Wytham Woods near Oxford. His methods were a mixture of direct observation, complimented by the use of automatic recorders. Additionally, however Hinde also made use of Trapping and ringing techniques – certainly something that reflected the influence of those at the Edward Grey Institute rather than Tinbergen's own influence.

Moynihan studied with Tinbergen from 1950 to 1954. He studied the black-headed gull using almost entirely observational methods in the field at Scolthead Island, Norfolk; Scoulton Mere, Norfolk; Ravenglass, Cumbria. His is without question the most austere of the Tinbergian works, eschewing anything outside of pure observation and field study, and with absolutely minimal intervention in the lives of the birds under study.

Chapter Three

In chapter three we looked at three of the more significant laboratory based workers, **Desmond Morris**, **Margaret Bastock** and the later work of **Mike Cullen**, (who had done his D.Phil. also under Tinbergen, but in the field some years previously).

Desmond Morris studied ten-spined stickleback in Tinbergen's laboratory. He arrived in 1951 and stayed until 1956, two years after he had completed his D.Phil. Morris worked on sticklebacks by trying to make the laboratory as natural as possible, and then spent the great majority of his research time for his D.Phil. in very close observation of the stickleback in large tanks. In the years after his thesis he worked on Zebra finches and Java Sparrows, observing them in large aviaries, a subject that was explored in chapter four.

Mike Cullen arrived in 1952 and his initial studies were very conventional Tinbergian work on the Arctic Tern, studied in the wild which he wrote up for his D.Phil. in 1956. Cullen stayed on until 1969, and it was later laboratory studies that this chapter examined particularly those on pilchard schooling. These studies made use of considerable trigonometrical techniques and also of still photography, but still were principally observational.

Chapter Four

Later work of the Tinbergians was the focus of this chapter, and it considered work from **Esther Cullen**, **Colin Beer**, **Hans Kruuk**, **Nick Blurton-Jones**, **Heather McLannahan**, **Desmond Morris** (again), **Richard Dawkins**, **Juan Delius**.

Esther Cullen arrived in 1952, but drifted away from research (Kruuk, 2003: 170). She had completed her PhD prior to her arrival at Oxford and so had no absolute submission dates. Cullen worked on kittiwake chicks on the Farne Islands, employing a mixture of close observation and very simplistic experiments with egg-swapping between kittiwakes and other birds. Hers was the first to consider evolution adaptation as a central part of the work.

Colin Beer arrived in 1956 and submitted his D.Phil. in 1960 after which he left for

Otago, New Zealand. Beer's work was entirely field based, working at Ravenglass in Cumbria. Beer worked on incubation and egg-shell removal studies in black-headed gulls, which involved both close observation and following that moderate experimentation by testing the responses of individual birds to different more or less egg-shell like objects. Beer's work was interested in possible implications for survival value.

Hans Kruuk arrived in 1960 but did not submit a thesis to Tinbergen, as he had already received a D.Phil. prior to his arrival in Oxford. Kruuk continued the egg-shell studies at Ravenglass begun under Beer, taking the observing and intervening approach also, with a similar focus on survival value, but continuing the studies and working alongside Tinbergen himself.

Nick Blurton-Jones arrived in 1958 and submitted his thesis in 1964. He worked on Great Tits at Wytham woods, near to Oxford. His studies involved testing Great Tit responses to different stimuli in order to understand which ones were the most significant. His work was done in the field using set up bird tables and stuffed dummy animals in order to consider the role of predation on survival value.

Heather McLannahan was present between 1967 and 1973 at the studied kittiwakes chicks at the Farne Islands, submitting her D.Phil. thesis in 1970. McLannahan took the cliff and egg swap studies undertaken by Esther Cullen and extended them, using perspex sheets in order to achieve better results in comparing kittiwake chicks and those of herring gulls, and their responses to the 'visual cliff'.

Desmond Morris was encountered again in this chapter, and his studies on Java Sparrows and Zebra Finches were considered. These studies sought to identify and explain the phenomenon of the supernormal stimulator, as discovered and demonstrated in roosting behaviour.

Richard Dawkins was one of Tinbergen's undergraduate students and began his D.Phil. thesis in 1961 and completed in 1964. His study was based entirely on laboratory research, using domestic chicks and studying each one only once. In each case he sought to ascertain innate preferences in the chicks by studying their pecking of coloured buttons in specially constructed laboratory boxes.

Juan Delius arrived in around 1960 and left in 1967, and his D.Phil which was

submitted in 1961. It is hard to be more precise as there is no extant documentation of formal arrangement for his supervision during his time studying for his D.Phil. The period following submission was the focus of interest for my study. This period was characterised by laboratory study of herring gulls, using vivisection and electrode stimulation of the brain in order to understand behaviours by understanding how they can be stimulated directly through electricity to the brain.

Appendix B: Tinbergen's Students a (nearly) Complete List

Tinbergen's Dutch Students

Tinbergen had at least three students in Leiden, from his time there, almost certainly there are more, but these are the only one's that I am sure of:

Student	**Date of Thesis**	**Animal(s) Studied**	**Title**	**Methods include**
Gerard Baerends	1941	*Ammophila campestris*	Fortpflanzungs verhalten und Orientierung der Grabwespe *Ammophila campestris*	Close observation and intervention, use of fake nests, and removal and introduction of food sources.
Leen de Ruiter	English Publication 1955 (thesis pre- 1949)	Jays and Puss moth caterpillars.	Published in English as Countershading in Caterpilars: an Analysis of its adaptive significance.	Camouflage in caterpillars. Caterpillars used as food in experiments to identify which shading combinations offered best protection.
Jan van Iersel	English Publication, 1953 (thesis pre-1949)	Three-Spined Sticklebacks	Probable English Title: An analysis of the parental behaviour of the male three-spined stickleback (*Gasterosteus aculeatus L.*)	Parental and reproductive behaviour, especially the identification of displacement activities. Close observation.

Tinbergen's Oxford Students

Tinbergen's Oxford Students, I have worked largely from the list of D.Phil.'s

submitted in Oxford at the time however where students of his can be identified who did not directly submit a thesis, but who were of importance to the group I have shown them too. The main anomalous student listed is Hans Kruuk, who did his fieldwork under Tinbergen, but was officially a student of University of Groningen. In addition Bill Russell and Robert Hinde are listed, as they were both closely linked to and influenced by Tinbergen, even though they were officially supervised outside of the group. I have not listed Uli Weidmann or Esther Cullen as I have not been able to establish where they had done his thesis prior to arriving at Oxford as a postdoctoral student or what work he definitively did whilst based at Oxford.

Student	**Date of Thesis**	**Animal(s) Studied**	**Title**	**Methods include**
Robert Hinde	1951	*Paridae* family	A comparative behaviour study of the *Paridae*	Close observation and intervention, use of automatic recorders.
Desmond Morris	1954	Ten-Spined Stickleback	Reproductive Behaviour of the Ten-Spined Stickleback	Close observation of the stickleback. Chosen because related to previously studied stickleback species
Martin Moynihan	1954	Black-headed gull	Some aspects of the reproductive behavior of the Black-headed gull and related species	Observation led non interventionist study.
Margaret Bastock	1955	Drosophila melanogaster	An analysis of mating behaviour in Drosophila, with special reference to isolating mechanisms	Observation led laboratory study
A.D. (David) Blest	1956	Eyed hawkmoth	The relation between birds and insects with false warning colouration	Observation and stimulation to monitor stimulation-response behaviour.
Mike Cullen	1956	Arctic tern	A Study of the behaviour of the Arctic Tern (Sterna macrura)	Close observation based on fieldwork
Aubrey	1956	Honey Bees	Published as	Observation

Manning			both: 'Some Aspects of the Foraging Behaviour of Bumble-Bees'; and 'The effects of Honey Guides'	and intervention, using model flowers to test the significance of certain stimuli to bees in natural surroundings.
Rita White/Weidmann	1956	Black-headed gull	The social behaviour of the Black-headed gull with special reference to incubation and food-begging behaviour	Close observation, also use of models and cards to measure stimulation levels.
M.F. (Fae) Hall	1958	Stickleback	A comparative study of the reproductive behaviour of the sticklebacks, Gasterosteidae	Observation led laboratory study.
Colin Beer	1960	Black-headed gull	Incubation and nest-building by the Black-headed gull	Egg-shell studies with an adaptationist perspective. Interventionist experiment with dummy eggs.
Gilbert Manley	1960	Black-headed gull	Agonistic behaviour of the Black-headed gull, Larus ridibundus	Observation and description of displays of the black-headed gull.
Juan Delius	1961	Skylarks	Das Verhalten der Feldlerche (Groningen but fieldwork under Tinbergen at Oxford.)	Observational fieldwork led

Nick Blurton-Jones	1964	Great Tit	Motivation studies with birds : with special reference to conflict and thwarting	Observational studies, but with introduction of dummy predators.
Hans Kruuk	1964 (published in *Behaviour*)	Black-headed gull	Predators and anti-predator behaviour of the black-headed gull (Larus ridibundus L.)	Egg-shell removal study. Observation tested by egg-shell study
Ian Patterson	1964	Black-headed gull	Timing and spacing of broods in the Black-headed gull, Larus ridibundus L	Observation and measurement of Black headed gulls.
Richard Dawkins	1966	Domestic chick	Selective pecking in the domestic chick	Highly interventionist laboratory study.
Michael Henry (Mike) Hansell	1966	Caddis fly larvae	An investigation of the house building behaviour of Trichopteran larvae	Observation of both caddis flies and their nests.
Mike Robinson	1966	Large number of stick insects and related species	Anti-predator adaptations in stick- and leaf-mimicking insects	Observations from fieldwork, in Smithsonian Tropical Research Institute under Moynihan.
Harvey Croze	1967	Carrion Crow	Dispersion in camouflaged animals and searching image in predators (or, Searching	Observation led field study with dummies and models tested.

			image in the Carrion crow and some anti-predator adaptations in camouflaged prey)	
Robert D. Martin	1967	Tree Shrews	Behaviour and taxonomy of tree-shrews (Tupaiidae)	Observation led field study.
Mike Norton-Griffiths	1968	Oystercatchers	The feeding behaviour of the oystercatcher, Haematopus ostralegus	Observation led field study.
Heather McLannahan	1970	Kittiwake chicks	Studies of Behaviour Ontogeny in Gulls	Kittiwake chicks on the 'visual cliff'.
Larry Shaffer	1971	Birds, several species	Specialisations in the feeding behaviour of gulls and other birds	Observation and filming of observations.
Iain Douglas-Hamilton	1972	African elephant	On the ecology and behaviour of the African elephant	Observation led field study. Based on close study when possible.
John Ramsey Mackinnon	1972	Orang-Utan	The behaviour and ecology of the orang-utan, pongo pygmaeus, with relation to the other apes	Observation led field study.