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Attempted Solution to a Fundamental Psychobiological Problem

How to Determine Individual and Milieu
Parameters from Species-Typical Behaviour
of Animals in Their Natural Environments

by Iven Reventlow

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Attempted Solution to a Fundamental
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Abstract

Iven Reventlow's research sets out to find descriptive models for hierarchically organized behaviour using the relatively simple behavioural repertoire of the three-spined stickleback (*Gasterosteus aculeatus* L.) as a test case, but with potential generalizations to other species, including humans. In collaboration with statistician Georg Rasch, Reventlow arrived at determining, for the first time in the study of behaviour, the relative effect upon a resulting, observed behaviour from the animal's sensitivity, motivation etc. (individual parameters) on the one hand, and those of the natural environment (milieu parameters) on the other.

Of special interest for the psychobiology of sticklebacks are his results concerning the motivational systems, that ethologists presume control the overt behaviour, as he presents experimentally based arguments for the existence of a third autonomous motivation-system for the male stickleback's building and maintenance of its nest which, together with the previously established two primary systems for reproduction and territorial defence, better explains the existing results than the ethologists' two-system's motivational hierarchy alone seems to be able to do.

As something also new, compared to traditional ethological methods, Reventlow presents a mathematical two-parameter model for the temporal development of motivation during an ongoing activity for the individual fish.

The ensuing Commentary and Postscript by Professor Jens Mammen address a number of problems inherent in the employed model and concludes that a 'waiting-time' model of the Weibull-type would be more advantageous for calculating the parameters and thereby quantifying the interaction between the individual and the milieu.

In fact this issue was intensely debated at the time in connection with the empirical investigations and raised some basic questions about demands to mathematical models and to collaboration between mathematicians and other scientists which were not fulfilled, leading to suboptimal conditions for the research project.

Count IVEN REVENTLOW† Dr.phil.

Invited lecture, entitled '*Aggressiv adfærd hos dyr og mennesker*',
in the Academy 6-IV-1982.

Attempted Solution to a Fundamental Psychobiological Problem

How to Determine Individual and
Milieu Parameters from Species-Typical Behaviour of
Animals in Their Natural Environments

by Iven Reventlow

Edited and translated by Arne Friemuth Petersen
With a Commentary and a Postscript by Jens Mammen



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Editorial Preface (2018)

A personal motive for the investigations to be presented here is reflected in a reaction Dr. Iven Reventlow rendered to an article on differences between behaviour and action, contributed to a *Festschrift* that was presented to him on the occasion of his sixtieth birthday in 1986. Reventlow commented: ‘Human beings behave mostly like others of their species and rarely make deliberately reasoned actions – and when they do, it may at the end of the road lead either to freedom by invention and artwork, if things go as best they can, or to slavery with lies and tyranny, when the worst comes to the worst.’

What motivates people in their daily activities had interested Reventlow from early on, and kept him studying the history of religion during his first year at the university, before he turned to psychology in 1947. This was not so long after he and his family, like other members of the Danish resistance movement, had fallen victim to barbaric action in a Nazi prison camp during the last months of the Second World War. These atrocities and the great loss of his elder brother, Ludvig, who was executed by Gestapo, marked him for life, as can be learnt from his account, ‘Arrested by Gestapo’, written one year before his lamented death in 2003.

In the Laboratory of Psychology at Copenhagen University, which Reventlow frequented as a student for the Magister Artium, it was not long before its world-renown Professor Edgar Rubin noticed and hired him as an assistant for his ongoing research into visually experienced movement and velocity (pace) of objects in motion (in part, and with Reventlow’s contributions, published posthumously as Rubin, 2016). So it was then with Rubin that Reventlow first came to learn scientific method, and especially the kind of phenomenological analysis Rubin had developed in his groundbreaking research on visual perception of figure and ground, and factors of importance for the recognition of such figures, and thereafter extended to his methodology for studying the perception of real objects in motion, which required more than a modicum of craftsmanship and commonsense for experimental work.

In *Sections 2-4*, below, Reventlow gives a number of reasons for using ethological methodology in his later research, and for his choice of experimental animal – the three-spined stickleback (*Gasterosteus aculeatus L.*) – which came to serve him in his own methodological developments. (“Ethology” is the study of behaviour of animals in their natural environments.)

He learnt fish-care and maintenance in ‘Danmarks Akvarium’ in Charlottenlund, with Director Mogens Højgaard, and worked with psycho-pharmacologically induced changes of motivational states in animals at the research laboratories of A/S Medicinalco, Copenhagen, under Director Erik Jacobsen. Some of his early experiments with sticklebacks were carried out (1955-60) in the basement of poet Piet Hein’s ‘Rungsted Skovhus’, while those reported here were performed from 1960 onwards in a newly acquired house in Rungsted. The practical side of this experimental work is related in Reventlow’s dissertation, 1970.

The object of this experimental work was to pursue the studies of hierarchically organized motivational systems of behaviour, initiated by ethologists in the 1950s, in order to develop methods for studying motivational systems in humans. Reventlow worked with Tinbergen’s and Nelson’s ideas about hierarchies, the so-called ‘embedding hierarchies’ – subsequently distinguished by Nelson (1973) from ‘hierarchies of connection’: a *hierarchy of embedding* implies that lower-level elements make up higher-level entities, which may then influence or control the lower-level elements; for example: a soldier is part of his platoon, but he is not part of the platoon-commander, should there be one as *hierarchies of connection* or ‘boss-ships hierarchies’ require. Reventlow’s experimental results indicate that the ethologists’ thesis of two higher-level motivation systems for explaining the occurrence of various behavioural forms in male sticklebacks during the initial phase of their reproductive period is insufficient, and necessitates the introduction of a third system of motivation for nest-care behaviour. However, of more wide-ranging importance is his use of time-measurements of the duration of the various behavioural forms, which made possible a determination of the individual parameters of each animal and the milieu parameters specifying the stimulus-situation. Such quantita-

tive determinations also slightly changed the focus of this kind of research, since one could now emphasize its purpose as follows: (1) to determine how often a motivational system occurs and how long it remains activated; (2) to determine the various ways in which the one and same motivational system may come to behavioural expression.

This progress was made possible by applying a so-called ‘description-model’ or ‘model of measurement’, one of the now famous *R-Models*, developed by the Danish statistician Georg Rasch and his collaborators. Such models had first been developed and used by Rasch (1960) in determining, on the one hand, the individual parameter for a subject’s possibility of answering questions correctly in an intelligence or attainment test (the subject’s ability or ‘*prority*’) and, on the other hand, the milieu parameter referring mainly here to the difficulty (or ‘*exposition*’) of the questions posed. With regard to the standardised test-situation, the great interest in these models can be found in the subsequent works by Rasch (1961), Andersen (1966), Christiansen & Stene (1968), Stene (1967) and Petersen (1967). In the 1960s Rasch applied steadily his ideas about measurement to more complex situations, where human and animal subjects encounter environmental problems of various kinds, and, as a consequence, react in ways typical of the individual, typical of the species, and typical of the problem-situation, still with the aim of determining the parameters of the individuals and the parameters of the milieu on the basis of exact measurements. These and related questions were debated by philosophers, mathematicians, psychologists, linguists, and computer scientists in a study circle on ‘Problems of objectivity’ which met in the Institute of Statistics, University of Copenhagen, invited by Rasch during the years 1967-68, giving rise to a report well over 400 pages (Rasch, 1968), later condensed and transformed by Rasch (1976) into his definitive *theory of specific objectivity*.

At one point in this study circle (*op.cit.*, pp. 148f.), there was a discussion as to how one could possibly calculate the individual parameters of animals that live more in symbiosis with their habitat than humans in test-situations, since most animals contribute actively to their ecological niche, for example by building a nest. Re-

ventlow argued that it might take quite a time to obtain ‘pure’ individual parameters of such animals, as their parameters would invariably include factors from the animal’s milieu, which at present, or perhaps forever, would remain unknown to us. As related in *Section 9*, the Commentary and Postscript, below, about five years went by with regular discussions of such problematic questions between Rasch, Reventlow and Jens Mammen before a satisfactory model, capable of analysing the available time-measurements of various forms of fish behaviour, arose.

This is true as far as the statistical model developed, a theoretically well-founded generalized model for ‘waiting times’, much more exactly matched the observed distributions of time-measurements than traditional methods based on a priori assumption of normal distribution, and accordingly on a priori assumptions of mean values and standard deviations as reliable parameters. Other problems arose, however, when the choice had to be made between different, but empirically equivalent, ways of defining the parameters of the new model. But this is another story to be told in the below Commentary and Postscript.

This was advanced methodology even for experimentally working ethologists, which I was to learn when shortly after, in 1968, I came to Oxford to study ethology with ‘Animal Behaviour Research Group’ and its founder, Professor Niko Tinbergen. Backed up by a detailed explanatory letter, I had once occasion of labouring out for him the statistical methods used in Copenhagen for analyzing the behaviour of sticklebacks – to which he just replied: ‘*You see, over the years we have found it quite sufficient to calculate the means of the distributions and, at most, to make a χ^2 -test.*’ – This was five years before the Nobel Prize!

So, with his insight and courage, and the new methodological tools at hand, Reventlow was able to answer Nelson’s 1973-question, ‘*Does the holistic study of behaviour have a future?*’, in the affirmative even before it was officially asked.

Arne Friemuth Petersen

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Iven Reventlow:
Psychological Analysis of Behaviour by
Means of Statistical-Ethological
Studies of Fish (1968)

The research presented here has aimed to develop and test exact methods for studying complex psychobiological phenomena without reducing their number of significant factors. The experiments carried out in this connection therefore mainly demonstrate the methods rather than report new results of interest for the sciences of fish as such.

1. Problems of Method in Studying Complex Psychobiological Phenomena

The classic method of keeping constant or leaving out all factors except one, in order to determine the effects of this independent variable on what is observed, has until now been used to a greater extent in natural sciences rather than biology and psychology, no doubt because it is easier to apply to 'lifeless' rather than 'living' phenomena. Perceptual 'Gestalt'-phenomena may illustrate why this might very well be so.

Gestalts are kind of 'wholes' known from everyday life, and shown by perception psychology to be organized functional phenomena. They arise through a complicated, multifarious interplay between sub-ordinary parts that again make 'wholes' of a similar complex and multiform nature. Examples of a somewhat daring type are human sexual gestalts that consist of parts on different perceptual modalities in the form of 'lower level' sign stimuli which, one by one, or together, depending on the entire situation, may be sufficient for releasing the appropriate reaction: These sign stimuli again constitute 'wholes' with their own elements on separate sensual modalities lower down the scale. There may be different ways

in which the parts interact to form a gestalt, as there will be different forms of functional wholes which may not all be considered as gestalts by psychologists.

So, instead of simplifying phenomena in the classical manner, it will be closer to the existing levels of complexity to investigate natural, biological situations in which more factors interact and vary at the same time. Thereby one is not likely to go into work with distorted or quite different phenomena. Among complex everyday situations it is, of course, important to choose the simpler ones. For example, situations where the experimental animal carries out its species-typical activities without having to learn something new, and where it is possible 'passively' to exclude factors that, say, occur only casually. This passive form of exclusion of factors is principally different from a mere 'active' exclusion of factors in experiments, in which one wants to study the effects of one factor at a time.

The following account sets forth and discusses methods for studying relatively complex psychobiological phenomena in their totality.

2. Ethological Approach to Complex Behaviour in Test-Situations

The request for methods to study everyday psychological phenomena, and not just what occurs in psychological laboratories, has been with me for a long time. The experimentation reported below was in fact provoked by experiences with human behaviour I had as a student when functioning as a military psychologist.

During routine examinations of aspirants for a training course as pilots, we found a characteristic syndrome that appeared to me interesting. In some psychomotor tests, a number of aspirants used stiff, spasmodic movements indicating that they were muscularly highly tense (Tranekjær Rasmussen, 1964); they also flushed easily and seemed, on the whole, nervous during the examination. The same aspirants revealed many comparatively 'neurotic symptoms' in the personality test. At the end of an interview for about an hour, we tried to roughly assess how muscularly tense this type of aspirant would be. As it turned out, they proved to be particularly stiff and

tense, and it was surprising how easy it was to release emotional outbursts from them, for instance fear and anger; it was enough to make them lie down, ask them to relax, and perhaps help them to relax by shaking their arms and legs.

These traits were found so often together in the same aspirant that it was reasonable to suppose that there was a connection between the symptoms, and since about 20 percent of the aspirants were registered as belonging to this type, it seemed to me important to go deeper into the matter. On the other hand, it was also evident that it would be difficult to find a scale of comparable figures for the different symptoms - the symptoms, as we observed them, all seemed to be parts of larger entities, and therefore difficult to compare precisely. For this reason it might be tempting to try to break these entities down into fragments in order to reach some comparable units. The best approach, of course, would be to find a unit which characterised the aspirant and which might manifest itself in different ways, according to the stimulus situation. This meant that the behaviour in every single test would have to be described in such a way as to make it possible to see, which details characterised the test, and which details characterised the aspirant; then it might be possible to built up new, mutually independent units that characterised, respectively, the individual test and the individual aspirant. (This, of course, is always the purpose of testing, but I had the impression that most analyses of test results stopped at too early a point.)

It appeared evident to me that the traits mentioned in the aspirants were expressions of something very comprehensive in their personalities and built up through long periods of time. Therefore it did not seem possible to arrive at profitable and practicable methods for doing reasonable, precise studies of such phenomena. If the phenomena were to be studied, it would then be necessary to find them in simpler contexts more easily accessible to investigation.

The phenomena observed in the aspirants - particularly the emotional outbursts they expressed when tested for muscular tension - could very well resemble what Trygve Braatøy (1945) had found in his patients when, in response to imposed muscular relaxation, they produced similar reactions, despite the fact that these pa-

tients had not manifested such emotional reactions themselves in spite of often violent influences. Braatøy thus concluded that the patients came to react with terror and obscene movements in the therapeutic situation, because they had formerly 'restrained' themselves from executing such behaviour in 'appropriate', everyday situations.

Braatøy's descriptions also resembled observations of certain behaviour patterns in animals reported by Konrad Lorenz, Niko Tinbergen and other ethologists. They had for instance seen how animals that, for one reason or another, had not found outlet for 'an instinctive act' would manifest the instinctive behaviour even in the absence of adequate biological releasers - psychologists would speak of 'emotive behaviour' in this case, Braatøy of 'primitive reactions', and the ethologists about 'vacuous or displaced activity'. In addition to such displacement activity, there are other important similarities between Braatøy's descriptions and those of the ethologists, as will be discussed presently.

Similarities of this kind made me wonder whether an ethological approach and observations on animals could throw any light upon the problems to which the examination of pilot aspirants had drawn my attention.

3. Some Fundamental Ethological Principles

Ethology provides a coherent theory of behaviour, which, in a simple way, integrates the stimulus situation, the motivational state and behaviour of the animal. The theory, which simulates very well what most psychological theories have attempted to do, may be represented diagrammatically as shown in *Figure 1*. The figure depicts the genetically determined connection - the 'innate releasing mechanism' ('IRM') - that ethologists assume exists between the afferent side and the efferent side of the nervous system, or between perception and behaviour. It is characteristic of the IRM-connection, that only certain components of the stimulus situation, normally found in nature, are necessary for the release of the behaviour; these components are called 'sign stimuli', from the German '*Schlüsselreize*'. Sign stimuli give rise to perceptions that work together with inter-

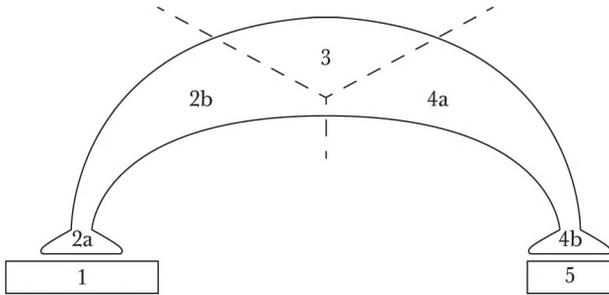


Figure 1. The figure illustrates how the ethologists imagine the functioning of innate realising mechanisms (IRMs). **1** indicates the external world of which a part may work as stimulus for a living organism, **2a** marks the organism's sensory organs, and **2b** the perceptual, or afferent, part of its nervous system. **3** represents the motivating and coordinating part of the organism's nervous system, **4a** the motor or efferent part of its nervous system, and **4b** its muscular movements. **5** comprises the organism's entire external behaviour. The arc, consisting of **2**, **3**, and **4**, shows IRM as an inherited neural connection, which causes certain stimuli, under the influence of internal motivating needs or drives - but without previous learning - to release the pre-programmed behaviour.

The idea of IRM implies that perception and internal states as well as behaviour always occur as a functional whole in ethological investigations. It should be added that the ethologists only rarely distinguish clearly between steps **1** and **2**. Here step **1** is drawn larger than **2a** to indicate that the perceptual systems of animals are not perfect physical registering apparatus, for which reason they cannot obtain information about all forms of manifestations of the physical world; an example of this would be animals without vision.

nally motivated conditions in such a way that the genetically determined behaviour is then released. When the interaction between these three main parts - perception, motivation, and behaviour - is disorganized in some way or another, phenomena may occur that resemble Braatøy's observations.

Sometimes several IRMs may be arranged into systems, as Tinbergen (1951) demonstrated for the male stickleback (see *Figure 2*, below). This system, and some of its related forms of behaviour, will be described later in greater detail.

However, let us first consider one example of an IRM, the courtship behaviour of the male three-spined stickleback. The initial phase of this behaviour consists of zigzag swimming towards a female stickleback on heat who has come into the male's territory. There are various stimuli which – in some fish – each and alone suffice to release the movements of the male; for instance, something with a conspicuous 'bulge' on the underside, like the swollen abdomen of a female in heat, or a short stick standing obliquely in the water may be seen to have the same effect on an approaching male as the position of a female. Results of some experiments I have undertaken, but too extensive to deal with here, cannot be interpreted in any other way than by saying that each single sign stimulus generates 'a visual gestalt', also known from human perception. With two sign stimuli at work there does not occur – as may easily be inferred from the literature (Seitz, 1940/41; Tinbergen, 1951; Lorenz, 1965) – a simple 'mosaic-psychological summation' of their releasing effects but, differently, an interaction, which is also of a Gestalt nature. It may be of interest to note that the sign stimuli of animals have similar functions, just as 'psychoanalytic symbols' appear to have for humans – or, more correctly expressed the other way round: 'psychoanalytic symbols' involve sign stimuli in human beings (see now Reventlow, 1972, where hierarchical links between the mere 'unit-like' sign stimuli and the more 'composed' Gestalts are succinctly described; ed.).

If it happens that the zigzag movement of the male stickleback is not released by a biologically relevant stimulus, it may be executed as a 'vacuum or displacement activity', so named by ethologists. Here reference can again be made to Braatøy, who (*op.cit.*, p. 297) observed copulation movements '*in vacuo*' in patients (also patients not being under treatment at the time) and fear reactions occurring in quite neutral situations, if only the patients got slightly relaxed or, in other words, to a lesser degree 'inhibit' their 'primitive reactions' in being carried out.

When the zigzag movement is not carried out, many other IRMs may be in function. This can be seen when the male stickleback is placed in front of its newly built nest, where it may occasionally carry out 'fanning'-movements which, although of importance for

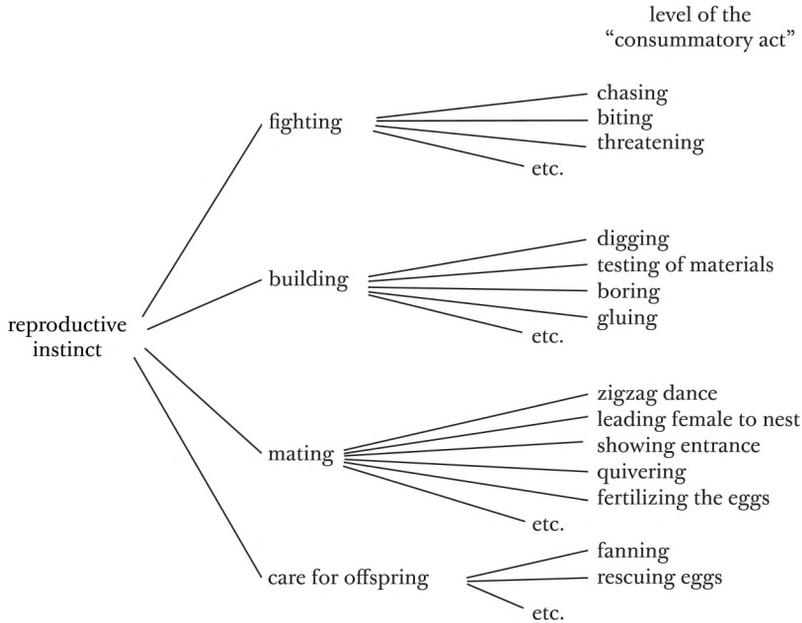


Figure 2 (after Tinbergen, 1942, 1951). The figure shows how the various common behavioural forms of the male three-spined stickleback can be arranged into a hierarchical system according to a biological point of view. The different forms of behaviour (for examples, see Section 6, below) are first integrated into sub-groups like ‘fighting’, ‘building’, etc., which are then comprised into a more comprehensive group, ‘the reproductive instinct’. The present investigation will *inter alia* touch upon the problem as to how this division may be viewed from a psychological point of view, since a biologist and a psychologist may not arrange the same observations into the same system in a similar way, or do it by means of the same methods.

the maintenance of the nest, have their most important function in connection with the male’s later care of its offspring (see ‘fanning’ in Figure 2). Their situation appears to be much more complex than what is conveyed by Tinbergen’s diagram, for although, admittedly, there is a basic connection between ‘fanning’ behaviour and the underlying parental motivation, the very same movements – when executed at an early stage of the reproductive cycle – will be stirred by other needs. In both situations, however, ‘fanning’ movements may come to expression if one or the other need cannot be satisfied right

away. Such 'displacement movements', which the ethologists profess are brought about by a strongly built-up need that lacks an adequate releaser will therefore easily come to expression with a 'displaced' behaviour.

In returning to Braatøy, a number of his patients complained about fear of flushing, or about a more general fear, tiredness and other 'primitive reactions' - in ethological parlance, 'instinctive behaviour' - which, during treatment by means of relaxation, appeared more or less to form a cover over other primitive or instinctive acts, for which reason it would be tempting to talk about 'displacement reactions' in these cases too. Add to this the similarity between Braatøy's other observations of 'vacuum activity', the resemblance between sign stimuli and symbols - and the fact that both ethology and dynamic psychology have found that, with increasing motivation, more and more stimuli may have a releasing effect on 'instinctive behaviour' - then one begins to suspect that there is, regarding these phenomena, a fundamental and comprehensive conformity between Braatøy's psychoanalysis and ethology.

In some earlier works (Reventlow, 1954, 1955, 1956), I made a closer analysis of these similarities and argued in favour of the hypothesis that the phenomena described by the ethologists and by Braatøy are closely related, and sometimes even identical. Similarly, Fletcher (1957), Russell & Russell (1961) and others pointed out numerous common traits in human and animal behaviour, thereby providing substance for the hypothesis that constitutes the basis of the present investigation. With this in mind, the methodology of ethology presents itself as an obvious choice for comparing, in a systematic way, certain animal behaviour with the 'primitive reactions' of the pilot aspirants and psychiatric patients discussed here.

4. Choice of Experimental Animal

In ethological experimentation, where innate forms of animal behaviour are studied, one is dealing with phenomena that change very little with experience, *i.e.* it is possible to conduct repeated experiments with the same animal without it changing noticeably -

while in learning experiments one studies animals that undergo change.

Working with animals, for instance the stickleback with which I have chosen to work, it is possible to provide the animal with its natural conditions of life during the experiments, and thereby not artificially remove important factors, as often happens in psychological experiments and tests with human subjects. In this way one may thereby study the total behaviour of the individual animal in its entire natural life situation. This is of importance, since we are not yet able to determine the fundamental concepts of psychology with any degree of precision, but have to work with vague ideas about perception, need, motivation, etc.

One may also interfere discretely with the animal and introduce the experimental factors one wants to investigate in this natural environment. In many cases, the number of such factors may be assessed much more precisely than is possible for experiments with humans.

When for such or similar reasons psychologists decide to make use of animal experimentation, they far too seldom realize how important it is for arriving at possible solutions to their problem that they chose a suitable animal.

For instance, we see how the white rat is faithfully used in physiological, psychological and psycho-pharmacological experiments, seemingly for no other reason than conventions with regard to the use of just this animal species. The white rat is very well suited to many kinds of experiments, but it seems to me to be an artificial product - of surprisingly high standard - which has been developed to facilitate, say, physiological investigations. In the white rat one has a 'living physiological preparation' with reactions that are relatively independent of the emotional factors, which, from the point of view of the physiologist, can only be inconvenient and a source of error. To obtain such a 'preparation', the white rat has been in-bred, and the result is an animal adapted to a life in the laboratory; it is also an animal largely without social behaviour and therefore easily put together with other individuals of the same species on a very small territory, compared with that of the wild rat; this means

that only little is left of the wild rat's strength, aggression, social behaviour, emotions, etc. The white rat is neither very aggressive nor very timid, and furthermore it seems relatively insensitive to pain. So, in all, it is easy to deal with for keepers and experimentalists. To this should be added that the white rat's need of motility is incredibly reduced, for which reason it can spend its whole life in a tiny cage without being visibly tormented. One has thus obtained a 'handy' animal for breeding centres and experiments, as it is emotionally rather blunt in comparison with its non-domesticated cousin. White rats are most often used in experiments concerning psychological problems without a reasoned consideration about its suitability for the problem at hand. For example, Levine & Mullins (1966) have shown that laboratory rats living in impoverished environments do not develop a complex endocrine system, which should be taken into account in studies on biochemistry, behavioural hormonology etc. Such drawbacks could perhaps be avoided to some extent if the very young animals were allowed to grow up in a more complex and natural milieu before they participated in experiments (Scott, 1968, Ch. 6).

There were several reasons for my choice of the three-spined stickleback (*Gasterosteus aculeatus L.*) as an experimental animal in the present study:

- (1) The behaviour of the stickleback had already been described in great detail by ter Pelwijk & Tinbergen (1937), van Iersel (1953), Tinbergen (1951), and Tinbergen & van Iersel (1947).
- (2) This behaviour is so varied that it has been possible to elucidate many psychological phenomena by analysing it.
- (3) The behaviour is thus very well suited to experimentation with the phenomena of interest in the present context, as outlined above.
- (4) The forms of behaviour under investigation here would be practically independent of learning processes.

(5) The behaviour is influenced only by a few ‘motivational factors’ such as aggression, sex, parental care, fear, and a few others.

(6) Sticklebacks are relatively easy to come by and provide with ‘natural’ life conditions.

These were the main reasons that made me choose the stickleback as an experimental animal. I did not, however, take into account the scepticism that the results from my experiments with sticklebacks would meet with in psychology, where such fish are rarely used in experimentation. In this respect, scientific psychology is quite different from other biological disciplines, where results obtained with sticklebacks are not considered curious or special. This, unfortunately, is the case in psychology, even when the research is carried out mainly for methodological reasons.

In spite of this, biological and methodological considerations favoured the choice of this experimental animal for developing ways of analysis of use in investigating the ‘everyday’ human phenomena introduced above.

There still remain a few questions regarding certain aspects of the behaviour of sticklebacks, as well as the choice of a measuring-model for analysing the behavioural data obtained – for, in fact, before one knows this kind of model, it is not possible to specify which aspects of behaviour should be recorded. These two topics must therefore be dealt with first.

5. Initial Experiments with Sign Stimuli

Before applying ethological methods to investigate phenomena related to personality psychology, which had originally intrigued us, I found it necessary to go into the perceptual problems of the so-called ‘Law of stimulus summation’ (German, ‘*Reizsummenregel*’ in Seitz, 1940-41; Tinbergen, 1951; Lorenz, 1965.) The ethologists express with this ‘law’ that if several sign stimuli can release the same behaviour separately, then their releasing effects will be additive when they occur simultaneously. The idea is that they act indepen-

dently from each other, since they are supposed to constitute a mosaic of independent sensations. If, indeed, the perception of sticklebacks worked in this way, then one could fear that their psychology was so widely apart from that of human beings that they could not be used as an animal of comparison in an investigation with the aim of throwing light on personality traits in humans.

Fortunately enough, a rather simple experiment made it possible to test the validity of the 'law of stimulus summation' in the stickleback. It consisted of an individual presentation of various dummies for some male sticklebacks; each dummy contained one or more sexual sign stimuli. When comparing their releasing effects, it turned out to be more complicated than expected, and as already mentioned above (p. 18), there was nothing in our results that could support the mosaic-psychological point of view implied in the 'law of stimulus summation'.

Apart from showing that there were several time factors to take into account, the results made it clear that sign stimuli, which release sexual reactions may also release various forms of behaviour at the nest, *i.e.* the same sign stimulus may release different forms of behaviour. The ethologists explain this phenomenon as 'displacement activity', which replaces the biologically adequate behaviour, because the appropriate releaser to a strongly built-up need is absent and therefore cannot give rise to biologically adequate behaviour (Tinbergen, 1940/41; Tinbergen & van Iersel, 1947). The missing adequate releaser is here, that the dummy - 'in response to the male's courtship' - should have followed the male down to its nest!

It is self-evident that besides the sexual releasers, the nest itself must also be of importance for the occurrence of patterns of nest-behaviour. In the experiments with dummies, we therefore obtained a rather confused picture with several independent sets of releasers at work (sexual and nest-care stimuli), which together may release the same forms of behaviour, which - on their side again - may replace one another in complicated ways. It therefore seemed advisable for me to analyse an even simpler situation before any final conclusion could be drawn on the experiments with dummies - namely, an experiment with the behaviour of an isolated fish towards its nest.

6. The Behaviour of Sticklebacks

When the male stickleback is in rut, its first impulse is to seek out a territory to be defended against other males, and in which it starts to build a nest. With the nest built, the male enters a long stable period, where it spends a large part of its time maintaining and improving the nest. In various series of experiments we studied the courtship behaviour of male sticklebacks during this period, in presenting them individually with a living female or, as mentioned above, with a female dummy ('mating' in *Fig. 2*, above), and also when they defended their territory ('fighting' etc. in the same *Figure*) against other males (Reventlow, 1961); the results were in accordance with those of the literature (van Iersel, 1953) in that there was a close connection between the sexual reactions of the individual male and its behaviour towards the nest. As resolved in the previous section, we started recording behaviour when the male had finished building its nest and was living isolated in an aquarium, which formed its territory - in other words, we arrived at experimenting with nest-care activity during the stable period, after the nest had been built and before mating had taken place.

The nest is built like a roof over a hole dug by the male in the sandy bottom. The roof consists of algae, plant residue, and similar things, often sprinkled with a little sand. In the roof there are a number of holes leading down to a tunnel that goes through the nest, and in which the eggs are to be placed by the female later during mating. The tunnel has a clearly marked entrance at one end of the nest. When the male comes up to its nest, it usually stands obliquely in the water, with its body at an angle of about 30° - 45° , and its nose pointing directly towards the nest entrance, at a distance of about 2 to 4 cm. From this initial position the fish may carry out various behaviour:

(1) It may put its nose into the nest-entrance and make a characteristic movement that seems to free the opening of loose nest material; this behaviour is called '*nest-boring*'. (The designations here are mainly due to van Iersel, 1953, included in Tinbergen's *Figure 2*, above.)

(2) Nest-boring may increase in intensity, so that the fish finally wriggles through the nest, with a similar movement to when it fertilizes the eggs laid in the nest by a female. However, when this behaviour has been carried out for the first time, the ethologists consider the nest-building phase as terminated. This behaviour, named '*creeping through the nest*', is also carried out during the stable period: at the most with less than an hour's interval, and at the least with a couple of days' interval (or more in the fish used here; the sticklebacks used by Nelson (1965) crept through their nest much more frequently), and, as will be shown later, during the following time this behaviour pattern has a great influence on the male's behaviour in general. For no sooner has a male crept through the nest before it invariably leaves the nest.

(3) Before or after '*nest-boring*', the male may perform the characteristic '*fanning*' behaviour, as it remains in the starting position making backwards movements with the pectoral fins and forward movements with the tail, thereby sending a strong water current through the nest. This behaviour, which has its main significance when there are eggs in the nest, is then performed to such an extent that there will always be sufficient oxygen in the water in the nest for the need of the eggs. Before there are eggs in the nest, '*fanning*' enables the male fish to check whether the roof over the tunnel is securely fastened and sticks well together. If some pieces of nest-material flap, when '*fanning*' is being carried out, the fish will interrupt the behaviour immediately and initiates:

(4) The so-called '*pushing*', a behaviour where the male stands vertically over the nest, and, with open mouth, repeatedly pushes the nest-material firmly down.

(5) The male may also execute a movement very similar to '*nest-boring*', with the only difference that it is carried out vertically down through the holes in the roof; this behaviour is called '*vertical-boring*', and it presumably serves to keep the entrances to the tunnel clear, so that water can flow freely through the nest when the fish produces '*fanning*'-movements.

(6) When 'vertical-boring' is carried out, the fish may sometimes carry out 'sucking' during which it sucks up sand from the bottom and scatters it through the gills over the nest, thereby making it stand firmer on the substrate (cf. van Iersel, 1953, p. 16).

(7) The last behaviour to be mentioned here is 'gluing', during which the male slides over the nest in a characteristic movement, with head and tail bent upwards and, from a part of the kidneys, excretes a substance that stiffens in the water and thereby glues the nest-material together.

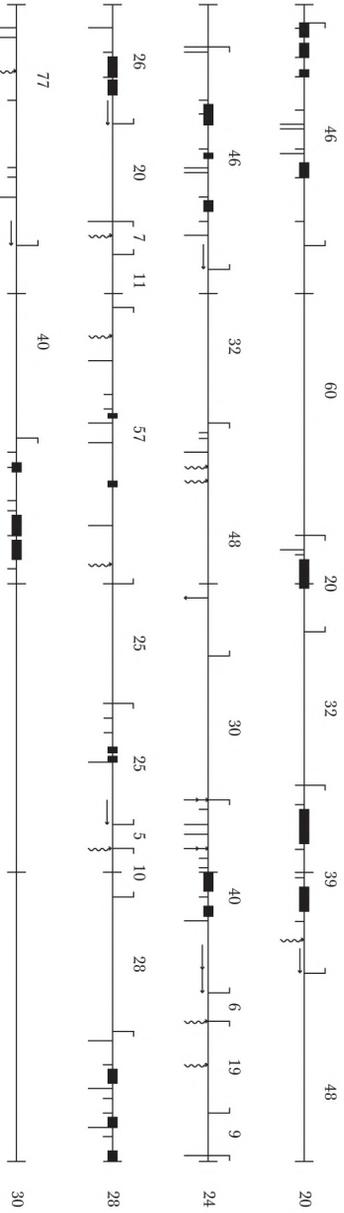
Although these forms of behaviour follow each other in roughly the order described here, no rigid pattern exists, and almost any succession may occur.

The duration of 'fanning' also changes rather much - from a single second to about 2 minutes. The first half of *Figure 3* represents diagrammatically the distribution of the different forms of behaviour with respect to time in a male fish that has lived under constant conditions for at least 24 hours. The diagram clearly shows how irregular the behaviour of such a male fish is. Even if one does not distinguish between the various behaviours, and only considers the length of time the fish stays at the nest, there is not much systematic behaviour to be found. This is also demonstrated in *Table 1*, which indicates the duration of how long a male fish is by its nest during an observation period of 30 minutes. At the beginning, we did not really know how to treat these many different kinds of behaviour, which seem to occur rather sporadically.

Behaviour at the nest:	10,	6,	1,	91,	20,	38,	88,	24,	3,	20,	70,	25,
	46,	20,	39,	46,	48,	40,	19,	26,	7,	57,	25,	10,
	77,	30										

Table 1. The table lists the number of seconds during which fish no. R2 261 18/10-1962 has been at its nest in the course of an observation period of 30 minutes. The first part of *Figure 3* gives a more detailed picture of the behaviour during the last 14 minutes of the same observation period.

R₀ 261 18.9.1962 at 1845



R₀ 261 18.9.1962 at 1921 (nest disturbed)

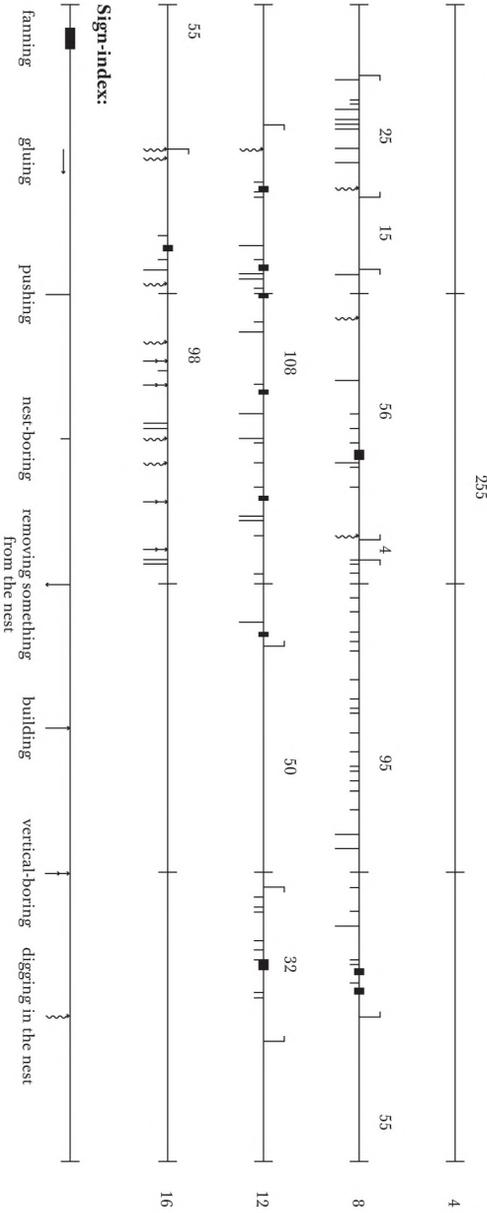


Figure 3. This figure gives a schematic representation of the behaviour of a male stickleback that occurs in a section of one of the series of observations reported in *Experiment 2*, where a fish is observed 30 minutes before and after its nest is *experimentally* disturbed. The section here includes the behaviour of fish no. R2 261 during the last 14 minutes before the experimental intervention and its behaviour during the following 14 minutes after the intervention. The different forms of behaviour are marked along a time axis, where each line contains 4 minutes of observation. '[]' comprises the time intervals, where the fish is at its nest, and the digits written over the time axis give the durations of the times spent by the fish at its nest or away from it. The behavioural forms are marked according to the list of signs that appear lowest on the figure.

Although the different forms of behaviour are performed in like manner by all males, it is nevertheless easy to distinguish a given male from the others and identify it alone from the frequency with which its different forms of behaviour occur. This being so, our problem would then be to find a model of description, which could simulate the occurrence of these different behavioural forms.

7. On Models of Measurement for the Behaviour Observed

We could, as mentioned, to a large extent, embrace and handle the factors of importance for the behaviour we observed. But no matter how well we tried to determine the conditions of the sticklebacks, and no matter how well we came to know the individual fish, we never arrived at predicting what a fish would do during the next seconds with any degree of certainty.

Chance so ordained it that, by this time Georg Rasch, professor of statistics at the University of Copenhagen and consultant at our Laboratory of Psychology, had just published his groundbreaking work, *Probabilistic Models for some Intelligence and Attainment Tests* (1960), where, on p. 11, my eyes readily stopped at the following passage:

Where it is question of human beings and their actions, it appears quite hopeless to construct models which will be useful for purposes of prediction in separate cases. On the contrary, what a human being actually does seems quite haphazard, no less than radioactive emission.

To turn to our attainment tests: We may give a problem to a pupil of whom we know that he could easily solve it, and yet he fails. Or we may give him a task, which is much too difficult, and anyhow he solves it. We can never know with certainty how a pupil will react to a problem, but we may say whether he has a good or a poor chance of solving it.

This way of speaking points to the possibility of mapping upon models of a kind different from those used in classical physics, more like models in modern physics – models which are indeterminist, where chance plays a decisive role: The possible behaviour of a pupil is described by means of a probability that he solves the task.'

Inspired by Rasch's success, we had to ask ourselves whether it would also be a good idea to leave behind the usual considerations of causality typical for psychology and, instead, employ probability considerations when analysing the time measurements of the behaviour of sticklebacks.

Some years after we had started work with the Rasch models, the same conclusion was made particularly clear to me in a discussion with the Norwegian psychologist Ivar Lie (1966), who illustrated the problem of predictability in psychological experiments as aptly shown in *Figure 4*. Lie was of the opinion that if either reaction R_1 or R_2 may occur, then something must be incomplete in the description of the conditions of the experimental situation, provided that there is a simple causal connection between the experimental conditions and the observed reaction. But is that really the only possibility? What if there is not such a causal connection, and that it is only possible to state *the probability* of the occurrence of one or other reaction? If – no matter how much trouble we endure – it still turns out to be impossible to predict whether R_1 or R_2 will occur, then it could be that the reaction may only be determined stochastically or, that there are so many almost equally important factors influencing the course of events, that it is impossible to register them all. The last point means that Lie's demand cannot be ful-

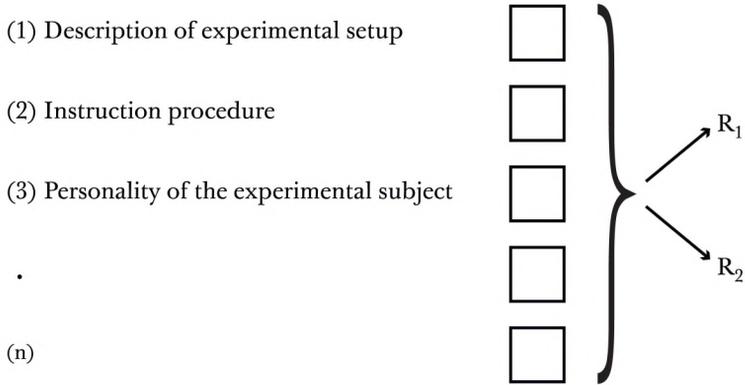


Figure 4. With this figure Lie (1966) illustrates his reasoning about the importance of the initial conditions for the results of an experiment. Lie maintains that if it is impossible beforehand to determine and predict whether result R_1 or result R_2 will occur, then it is due to lack of precision in the description of the initial conditions for the experiment (see further explanation in the text).

filled in practice, at least not at present. So no matter how the case stands, I arrived at the conclusion that it was most suitable to use probability models for treating our results, as we had, indeed, already started to do.

8. The Specific Probability Model

We had started work with the Rasch-models after having analysed some a priori assumptions about the phenomena under study and their mathematical representation in the models, thus the following two assumptions about the male stickleback’s behaviour at its nest:

Assumption I: The amount of behaviour may be described basically by means of durations, for example, how long a given behaviour is being performed without interruption.

ad I: This assumption does not imply that behaviour in general can be described exhaustively by durations alone, since behaviour may have other aspects – say, the intensity and vehemence with

which it is performed – aspects that are not so easily described in terms of ‘durations’.

Assumption II: The probability that a given behaviour will be interrupted within a short time interval is the same, irrespectively of how long the behaviour has already been performed.

ad II: This assumption is differently problematic in that a given behaviour, which has been going on for some time, may *either* continue *or* be interrupted, depending on the entire motivation of the animal – as expressed in Assumption II, which is also mathematically simpler and more practical in a number of ways; in the following, the probability that a behaviour will stop after a given time lapse is thus considered constant, and denoted λ .

Contemplating *Table 1* and *Figure 3*, a third assumption had to be introduced, namely:

Assumption III: The different forms of behaviour of a fish are stochastically independent.

ad III: This assumption implies that one behaviour must not influence a following behaviour – an example in our present context would be that of a male fish, which had once been at its nest for a short time, and then next time remained there longer, and at each of its following visits to the nest would be staying there for longer and longer periods of time.

With these a priori considerations in mind, we set out to find correspondence between the behavioural phenomena observed, our time measurements, and the model employed.

Whereas it is impossible to observe directly the probability that a fish will be changing behaviour within a given interval of time, it is nevertheless possible to estimate the value of λ on the basis of a number of observed durations for, say, a male fish’s nest-behaviour, using the following formula:

$$P\{t \geq T\} = e^{-\lambda T}, \quad (1)$$

which is a further development of the model used in Rasch (1960, Chapter III) to describe phenomena that satisfy *Assumption I and II*. The formula states the probability that a behaviour going on during a time interval t , which is larger than or equal to an arbitrarily chosen time-lag T (for example 10 or 100 seconds), may be calculated by means of the expression $e^{-\lambda T}$.

Here, e is an ordinary mathematical constant (2.718 - the base in the natural logarithm) and therefore without psychological interest. T is the length of time during which information is required; it may be chosen at will by the experimentalist, and does not in itself provide any psychological information about the observed phenomena. This is, however, the case for the parameter λ , which is the quantity that gives information about the psychological circumstances under observation: it will be dependent on the inner motivating forces of the individual fish, on the environment in which the fish finds itself, etc.

Let us now first assume that that we know the value of λ , that is characteristic of the behaviour of the fish under observation¹. This will enable us to calculate the probability whether the investigated behaviour is still being carried out or not, after the chosen time-lag of T seconds. In so doing it will be seen, that the larger λ is (*i.e.* the shorter the mean time is for the fish being at its nest), the smaller the probability will be, at any point in time, that the fish will still be at the nest, since for a larger λ , the quantity $e^{-\lambda T}$ will be smaller (or, as it can also be written: $1/e^{\lambda T}$); in other words, the larger λ is, the higher the tendency will be for the fish to have left its nest - which is the same as saying: the longer the time interval is for which information is required, the smaller the probability that the fish will still be found by its nest. This will hardly surprise many psychologists, since no behaviour continues perpetually without interruption -

1. An estimate of λ is obtained from $n/\Sigma t$, where n is the number of times the male fish has been observed by its nest, and Σt is the sum of the periods the fish has been observed at the nest; thus Σt is the total length of time the fish has spent at the nest. Therefore λ becomes simply the reciprocal value of the mean time the fish is by its nest.

but it nevertheless seems to contradict our *Assumption II*, which states the probability that a given behaviour will be interrupted is constant, independently of the length of time it has already been performed.

It is possible to arrive at an understanding of this apparent contradiction in different ways, among which the following may demand less mathematics:

Above we had the formula

$$P \{t \geq T\} = e^{-\lambda T}, \quad (1)$$

that gives the probability that a male fish will remain at its nest during a time-lag t , which is equal to or larger than a time-lag T chosen at random; since after this time-lapse there is 100 percent chance (the probability 1) that the fish has *either* left its nest *or* is still there, then the probability that the fish has left its nest before time-lag T has passed, will be

$$P \{t < T\} = 1 - e^{-\lambda T}; \quad (2)$$

in other words, this formula gives the probability that the fish will interrupt its nest-behaviour before a time-lapse of T seconds has passed.

From a psychological point of view, one might think that something special would occur just after the fish has arrived at its nest, for which reason it might be of use to have the probability regarding the first second. This can be obtained by inserting $T = 1$ in formula (1) and (2):

$$P \{t \geq 1\} = e^{-\lambda} \quad (3)$$

and

$$P \{t < 1\} = 1 - e^{-\lambda}; \quad (4)$$

regarding (4) one may add that it can be shown mathematically, that the smaller it becomes, the more $1 - e^{-\lambda}$ approaches λ . Therefore, for small values of λ , the formula (4) takes the following form:

$$P \{t < 1\} = 1 - e^{-\lambda} \approx \lambda. \quad (5)$$

However, it may be of particular interest to look at the formula that describes what happens in each of the short time-intervals, which, in our experiments with sticklebacks, constituted the unit of measurement of 1 second.

As before, we have

$$P \{t \geq T\} = e^{-\lambda T}, \tag{1}$$

which may also be written

$$P \{t \geq T + 1\} = e^{-\lambda(T+1)}. \tag{6}$$

Formula (1) states the probability that a fish is still at its nest after a lapse of T seconds – or expressed in a statistical way: formula (1) gives that fraction of the total number of observed fish (with the same λ), which are still at their nest after the lapse of T seconds, and formula (6) gives the corresponding fraction after a lapse of $T + 1$ seconds.

Since, as time passes, there are going to be fewer and fewer fish at their nests – because there will all the time be some fish leaving their nests – we may find the probability that a given male fish leaves its nest by the second that follows after T , in subtracting (6) from (1).

Thereby we obtain the probability that a fish will leave its nest after a time-lag t located between T and $(T + 1)$:

$$\begin{aligned} P \{T \leq t < T + 1\} &= P \{t \geq T\} - P \{t \geq T + 1\} \\ &= e^{-\lambda T} - e^{-\lambda(T+1)} \\ &= e^{-\lambda T} - e^{-\lambda T} \cdot e^{-\lambda} \\ &= e^{-\lambda T} \cdot (1 - e^{-\lambda}), \end{aligned}$$

and as $1 - e^{-\lambda}$ (4) converges towards λ for small values of λ , the expression can be changed into

$$\lambda \cdot e^{-\lambda T}. \tag{7}$$

This is incidentally the differential coefficient with regard to T of $1 - e^{-\lambda T}$, which is the formula that states the probability that a given behaviour has stopped at time T . The differential coefficient

$$dP\{t < T\} / dt = \lambda \cdot e^{-\lambda T}$$

or

$$dP\{t < T\} = \lambda \cdot e^{-\lambda T} \cdot dt \quad (8)$$

is also designated 'the probability density' or 'the intensity function at t '.

Formula (8) gives the probability of making an observation located between T and $T + dt$. As dt in (8) may be chosen as randomly small, formula (8) does not presuppose, like formula (5), that the value of λ is small. Since this difference is without significance for the resolution of the problems dealt with here, it shall be ignored in the following.

We can now see that the value of $\lambda e^{-\lambda T}$ (7), which gives the probability of a fish leaving its nest in some second (between T and $T + 1$) is the multiplication of the probability λ that the fish will be leaving its nest in the first second (5) after it has come to it, and the probability of the fish still being at the nest T seconds after having come to it (1). The last part gives the probability of the fish being at the nest, at a given time, and it does not say what it will do in the second that follows T , which is, however, what the first part does. This part, called 'the intensity', is thus constant (since λ has a definite value), and therefore independent of the time the fish has already been at the nest - which means that no matter how long a fish has already been at the nest, it will have the same probability of leaving it in the next second. It is thus not only the probability of what will happen in the first second, but also the probability of what will happen in any second. This means that the male fish have the same tendency to leave their nests in the second after the next, independent of how long they have already been there.

As this is exactly the same as the content of our *Assumption II*, above, we have thus received a positive answer to our question whether Formula (1) can be used to describe forms of behaviour that obey this a priori assumption - namely, that the λ , entailed in (1), corresponds to the λ which we use to indicate the constant probability that a behaviour will be interrupted.

And, at the same time, we have obtained a solution to the apparent contradiction we had in maintaining that there is a decreasing probability that a fish will continue a behaviour once begun, and at the same time asserting that there is the same probability that the fish will interrupt the behaviour, no matter how long it has already been carrying it out. The explanation is now simple: the probability that the fish will interrupt its behaviour in a certain second must be considered in relation to the number of fish which were still carrying it out when the second began. On the other hand, the probability that a fish will still carry out its behaviour after T seconds must be considered on the basis of the number of fish, who started it at all. Thus the contradiction is dissolved in realising that, as time passes, there will be fewer and fewer fish still carrying out the behaviour, but that it is the same percentage of those who have been doing it all the time who will stop it in the coming second.

Originally, when we tried to use Rasch's model on our observations of the behaviour of the male stickleback at its nest, it seemed quite reasonable to accept the first assertion: that, as time passes, there would be fewer and fewer animals still carrying out the same behaviour. On the other hand, as already stated, it seemed rather doubtful - indeed, almost unacceptable - that there should be the same probability that an individual should stop a behaviour no matter how long the behaviour had already been going on. To me it seemed a foregone conclusion that the longer a behaviour continued, the larger probability there must be that it stopped. But as the possibility of a decreasing probability could not either be accepted right away, we chose to work with the mathematically simplest assumption - namely that of a constant probability.

9. Reformulation of the Model

The first results we obtained by means of the model indicated that there was a constant probability that a male fish would leave its nest, no matter how long it had already been there. We checked the accordance between our observations and the mathematical model by means of a rather simple graphic test (see p. 38 and 110). As long as we looked at the check of the *individual* series of observations, each

arising from one fish at a time, the model seemed fairly acceptable, but when we compared the checks from all the series of observations, it appeared that there was a generally increasing tendency for all fish to leave their nests the longer they had been at them. That is, on the face of it, just what had been expected to be the most probable.

Therefore Rasch amended the model to be:

$$P\{t \geq T\} = e^{-\lambda \cdot T^\alpha}; \quad (9)$$

this expression includes the possibility that the probability changes as the behaviour continues. The material was therefore subjected to another graphic test (Rasch, 1964; Christiansen, 1965) the purpose of which was to decide whether the phenomena observed were of such a nature that the new formula could be accepted as a description of them. (It turned out that this new control was also to be preferred as a check on the first model which, to be acceptable, must have $\alpha = 1$; the control was carried out by means of a computer programme, Reventlow & Mammen, 1964, which at the same time estimated λ and α .) The new test revealed nothing that made it unacceptable to use the new generalised model.

The expression, which in the new model corresponds to the intensity λ in Formula (7), has the form: $\alpha\lambda T^{\alpha-1}$ (Rasch, 1964; Christiansen, 1965); as in the original model, it gives the probability that the behaviour will stop in the $T + 1$ second after it has started. Since λ and α are constant for a given observation, it is enough to consider how $T^{\alpha-1}$ varies to be able to judge how the intensity varies. So if $\alpha < 1$, then $\alpha - 1$ becomes negative, and therefore $T^{\alpha-1}$ becomes smaller and smaller the more T increases. If $\alpha = 1$, then it will make $T^{\alpha-1} = 1$, and the whole expression therefore λ , as in Formula (7). If $\alpha > 1$, then $\alpha - 1$ becomes positive, whereby $T^{\alpha-1}$ increases as T grows - or as time passes. One should note, that $\alpha < 1$ means that the probability of an interruption of nest-behaviour in a given second will decrease the longer the behaviour has been going on, whereas $\alpha > 1$ renders the reverse situation, namely that the probability will increase.

However, the generalisation of the model resulted in great difficulties. Truly enough, it was possible to estimate the values of λ and α ,² but it turned out to be very difficult to calculate whether they varied from one fish to another, or for each individual fish from one experimental situation to another, because the variance of λ was dependent on α . To this should be added that α which, as an exponent – and therefore, to a lay opinion, perhaps the most important parameter – was varying apparently quite randomly between 0.73 – 2.72, and without any obvious connection to the psychological circumstances.

The solution to the problems came as a surprise after numerous and extensive calculations, where it turned out that α did in fact not vary more than an observed constant of that magnitude was allowed to do from a statistical point of view. *We could therefore take α to be common to all sticklebacks, and the same in all situations we had worked with.*

The comparison of the different values of α was carried out by a χ^2 -test (with the help of the formula:

$$SK_w = \sum_{i=1}^k n_i w_i^2 - \left(\sum_{i=1}^k n_i w_i \right)^2 / \sum_{i=1}^k n_i,$$

which is χ^2 -distributed with $k - 1$ degrees of freedom, as $w_i = \ln \alpha_i$ and α_i is the α -estimate for the i -th series with $k =$ the number of observed series), into which went all values of α obtained from the different series of experiments. As the comparison made it acceptable to conclude that, until further results had turned up, α could be considered a psychological constant of an amazingly general character and, on the basis of 2255 individual observations, an estimate consisting of the weighted average of all α 's turned out to be 1.513.

This most welcome result made it possible to work with a model, which, from a mathematical-statistical point of view, corresponded very much to the original and simpler model, although used in a slightly modified form:

$$P \{t \geq T\} = e^{-\omega T^A}, \tag{10}$$

2. α is estimated from $\sqrt{0.31(n-1)/SKO-s^2/n}$ and $\log \lambda = -\alpha \cdot s/n - 0.2507$, where $n =$ the number of observations, $SKO = \Sigma (\log t)^2$, $t =$ time observations, and $s = \Sigma \log t$.

where $\mathbf{A} = 1.513$ and the change from λ to ω is only made to make it easier to remember the special form of the model now worked with. As \mathbf{A} is larger than 1 it means that the longer a fish has been at its nest, the greater probability there will be that it leaves the nest in the coming second – just what was originally expected from an immediate psychological consideration.

This means, however, that our a priori *Assumption II* must be rejected on the ground of the empirical findings, while it is now empirically possible to justify the assumption that *the probability that a fish shall leave its nest increases exponentially with a constant factor as time passes by*. There still remains our a priori *Assumption I*, that the amount of behaviour may be described relevantly by means of durations, the reasonableness of which the following experimental account shall hopefully testify – always keeping its limits in mind. Regarding our a priori *Assumption III*, that the durations of the different forms of behaviour are stochastically independent, no reasons so far have forced us to give up this supposition.

In Formula (10) it is easy to determine ω ,³ and to see whether it varies from one fish to the next, or from one situation to the other (for this, see *Experiment 2*, below).

10. Analysis of the Nest-Behaviour of Male Three-Spined Sticklebacks

With this we may have arrived at arguing in favour of the adopted ethological method of direct observation, the material of observation – the behaviour of fish measured in seconds – and an exact mathematical model of description, which now enable us to start working on the problems originally posed about some phenomena that Braatøy had called ‘primitive reactions’ and the ethologists ‘instinctive behaviour’, and which in all likelihood are closely related to a syndrome observed in pilot aspirants.

These problems initially described (above, pp. 14f.) may now be condensed to the following two main problems:

3. ω is estimated by $n/\Sigma t^{1.513}$.

(i) To analyse the behaviour into such small details or units that – according to certain criteria and psychological points of view – they may be included in larger entities, the construction of which would then be known.

(ii) To investigate how outer and inner conditions work on the larger entities as well as on the minor units from which the former are constructed.

In choosing to study the behaviour of the male stickleback during a period, when it has finished building its nest and waiting for a female ready to mate, we also seem to have selected behaviour patterns that ethologists have already analyzed in such detail that it may now be possible to try integrating them into larger entities, say, into behaviour forms for maintaining the nest and ‘other’ forms of behaviour.

Although it was the existence of such larger entities of behaviour that constituted the basis for our choice of mathematical model, things worked out in such a way that the chosen model, in its general form, only contained two parameters (λ and α). As already touched upon, the parameters must depend both on the inner state of the individual fish and the exterior circumstances. As we have found that α is the same (namely $\mathbf{A} = 1.513$) in all our experiments, we must conclude that α is also independent from variations in the individual as in the surrounding world – at least with regard to the factors we investigated in sticklebacks. Variations in individual or environment must then be investigated by means of ω , since ω must be the result of interplay between the factors that determine the occurrence of the behaviour. Thus the ensuing work will consist of analysing the variations in ω compared to variations in the state of the individual or the environment, in as much as it can be excluded that behaviour of such complexity, like the maintenance of a nest, should depend on only one factor, like ω in Formula (10). Therefore the only reasonable hypothesis is, that parameter ω expresses a complicated interaction between many factors, and that future work will consist of breaking down the parameter into components that reside in ω in ways corresponding to their effects on the behaviour.

The ‘sub-parameters’, found in this way, will then be expressions for what we today call ‘*individual parameters*’, and other expressions for what we call today ‘*milieu parameters*’ – to which may be added ‘sub-parameters’ which at present we are unable to place as either ‘inner’ or ‘outer’.

For the present we shall adopt Rasch’s parlance, where individual-dependent factors that determine the probability of the occurrence of a behaviour are called ‘*pronity*’, and the corresponding factors dependent on the environment are called ‘*exposition*’. Returning to the above problem formulation, our two main problems may then be reformulated this way:

(i) To investigate which part of the behaviour is determined by ‘pronities’, and which part by ‘expositions’, taking point (ii) into account.

(ii) To investigate how different behavioural forms may reasonably be integrated into larger entities, taking point (i) into account.

Experiment 1: Observation of Nest-Behaviour

The first experiment consisted of just observing 12 male sticklebacks individually at their nests for 30 minutes. *Table 2* shows the durations for observations of the activities ‘at the nest’ and ‘away from the nest’ for Fish no. R2 231 16/11 1962.

Behaviour at the nest:	1, 3, 1, 8, 2, 15, 42, 20, 8, 68, 44, 89, 4,
Away from the nest:	30, 39, 70, 27, 50, 96, 40, 50, 28, 5, 37, 3, 79,
Behaviour at the nest:	24, 51, 43, 51, 29, 9, 34, 2, 29, 31, 7, 48, 7, 4,
Away from the nest:	31, 56, 7, 8, 40, 14, 8, 75, 128, 99, 46, 4, 24, 24, 8

Table 2 gives the time intervals during which Fish no. R2 231 16/11-1962 was at its nest and away from it, respectively, in an observation period of 30 minutes (cp. *Table 1* and *Figure 3*).

It will be seen from the table, as well as from *Figure 3*, above, that the time a fish spends away from the nest is as irregular as the time it spends at the nest, just as the durations of the different forms of

behaviour seem to be stochastically independent, both regarding each form of behaviour as all of them taken together. Nor does there seem to be any connection between time spent at the nest and away from it. However, it turned out that the time a fish spends away from the nest could also be described with the model.

Unlike Tinbergen's 1948-results (1951, p. 59 and 61), our analysis does not show any periodical fluctuations in the nest-building activity - by Sevenster (1961) called 'fanning-cycles' - perhaps the reason being that our periods of observations are relatively shorter than theirs, and therefore cannot reveal such systematic variations in nest-building.

On the basis of our time measurements it is now possible to describe each individual fish's way of using its time for nest-behaviour. The results show - apart from a very small number of fish with a particularly limited behaviour at the nest - that there is no connection between the duration of the behaviour at or away from the nest (cp. *Experiment 3 and 4*). A given behaviour must therefore be described by both an indication of how soon it begins and how long it lasts, and there seems to be no connection between these indications either. Catlett (1961) entertained a similar division, however with regard to aggressiveness in mice.

When we examine the way a certain nest-behaviour, such as fanning, appears during the entire time of observation, we find that it occurs in a rather queer way and not at all as it 'ought to do', if it were to follow the chosen model. If, on the contrary, we do not take into account the time a fish has spent away from the nest, and only consider the total time spent at the nest, during the whole period of observation as a connected whole, then it turns out differently: considering, for example, what might be called 'time at the nest, when fanning is carried out' and 'time at the nest, when no fanning is done' then it appears possible to describe fanning behaviour with the help of the model. Here the probability is therefore conditional on the fish being considered as staying at the nest all the time.

The experiences from the analyses of fanning thus show that the existence of such behaviour at the nest must be considered as a conditional probability, where the condition is that only the time the fish spend at the nest is taken into consideration. This might seem

to indicate that in the different forms of nest-behaviour we have parts that could very well be included into a larger unit of 'behaviour at the nest'. Until now the different forms of behaviour have only been partly analysed, and only with the model in which both α and λ occur. The values of α , so far determined, do not deviate from $A = 1.513$.

Instead of continuing the analysis of the occurrence of the different forms of behaviour at the nest, we preferred to analyse various circumstances of importance for the probability of the occurrence of the more complex systems. In the following, such comprehensive systems will be designated in a concrete way, as no attempt shall be made at finding a general term for them. For even if reference is made only to the concrete behaviour observed, the systems may be designated in different ways, seemingly with the same content from a behavioural viewpoint, but which may be said to have different psychological connotations – for, psychologically, it is not quite the same thing to say that the fish 'stops its behaviour at the nest' as saying it 'starts other forms of activity than activity at the nest'. This vagueness contains the germ of some very thrilling psychological problems, which, however, shall be left unsolved here. The phenomena will thus be mentioned as if there were only one system 'in operation' or 'not in operation', and the comprehensive system in question includes behaviour at the nest, which we consider can be either 'on' or 'off'.

As far as we know at present, the existence of the different kinds of behaviour at the nest can only be described satisfactory if we only take into consideration the time the fish spends at its nest – *i.e.* only the time when the higher system is on, or comes to behavioural expression. The probability of the occurrence of the subordinate behaviour is thus conditional on the activation of the higher system. This means that in building up the hierarchical system, respect has been given to the way both the higher-level behaviour and the lower-level behaviour appear. Future research may show how risky it is to build up psychological systems on such a mathematical foundation, and whether it may lead to sheer difficulties. Until further results have been obtained, it may be possible to work in this way, accepting that the different subordinate behavioural forms can only be described satisfactorily on the condition that the primary system

is activated. If we suppose that the results of this way of working say something essential about the psychological mechanisms that condition the behaviour, then it means that we have obtained a new tool for the construction of psychological systems. When the point of departure for these investigations is taken into account, it is not surprising that the little bit of a system that has been built up here agrees on the whole with Tinbergen's scheme. However, the accordance may be understood as an indication that the different forms of behaviour are not only – as in Tinbergen's scheme – biologically subordinate to the comprehensive system (which means more precisely: constitute suitable parts of an integrated system of value for the animal's survival and leaving offspring behind), but that they are, in a fundamental way, psychologically subordinate to the higher-level system.

One of the problems for future research will be to find such psychological conditions. It will be most interesting to see whether the systems arrived at by means of statistical-psychological analyses will correspond to systems like Tinbergen's, that were set up according to biological view points.

Experiment 2: Experimental Disturbance of the Nest

When 12 male sticklebacks had been under observation individually for 30 minutes, a stick almost as thick as a fish was pushed through the tunnel of the nest, so that the nest would be brought in a condition corresponding to the state into which the fish itself would bring it when creeping through the nest. Each fish was then observed for 30 minutes again, and its behaviour recorded as accurately as possible.

On the basis of these observations, two alternative hypotheses may now be put forward:

(1) The individual fish have changed after the experimental disturbance of the nest with respect to both their tendency of *coming* to the nest and start nest behaviour and their tendency of *remaining* at the nest and doing nest behaviour.

(2) All fish have changed in the same way with regard to one or other of the mentioned tendencies.

Table 3 contains the results of testing these two hypotheses (in leaving out the results for Fish no. R2 C10 20/11-62; the reason will be given below). How the hypotheses were tested is explained in the table legend.

The *upper part* of the table gives the results for how long the male fishes are found away from their nests - that is, their probability of approaching their nest to start on nest behaviour in the next second.

As the total u_0 is 0.840 and thus less than 1.96, which marks the 5% level of significance, we must reject the hypothesis that the fish - considered as a group - have changed their tendency to start nest-behaviour as a consequence of the experimental disturbance of their nests.

Then, in considering the u_0 's for the individual fishes, we notice that Fish no. R2 231 22/11-62 has an individual u_0 greater than 1.96. Since a significance level of 5% implies, when no change has occurred, that one can expect a u -value larger than 1.96 in one case out of 20, then it will not be exceptional to find an excess-value of u in one out of 11 cases. Thus it is reasonable to reject the hypothesis that the fish changed the probability of initiating nest-behaviour after their nests had been messed up.

Looking next at the *lower part* of *Table 3*, which contains the results for how long the fish stay at their nests - that is, giving the probability of interrupting their nest-behaviour the next second - then the situation seems more tangled.

The total u_0 is well below the level of significance, which, for the fish considered as a group, implies that we must reject the hypothesis that their tendency for leaving their nests has changed. Furthermore, if we look at the individual u_0 's, then the results are even more confused, as 2 of the values are too high and 3 of them too small, while 6 values are under the level of significance. Since there are fish with increasing tendency and fish with decreasing tendency for in-

interrupting nest-behaviour, the results do not become clearer if we test the hypothesis, that *all* fish change with the same factor – the vertical column over \mathbf{u} also shows, that the picture is no clearer, even when we test the hypothesis that all fish have changed with the total of δ .

From the general result we must therefore conclude for the present that the state of the nest – its appearance or ‘exposition’ – has no influence on the probability of initiating or interrupting the fishes’ nest-behaviour.

It is not possible to point to factors that may be responsible for these variations – other than that some of the nests had been messed up more than others, or that some of the fish may have been more scared by the interference than others. However, our data cannot enlighten matters any further.

Still, this may be the place to explain why the result from the experiment with Fish no. R2 C10 20/11-62 has not been included in the final calculations. As alluded to above, due to the three consecutive messing-ups of the nest for this fish, it became clear afterwards that the experiment had ‘gone fishy’ and ought to be excluded. At first, however, I did not leave out these results and treated them like the others, but some time later, at a conference about statistical questions, Georg Rasch caught sight of the results and exclaimed that some error must have occurred with this experiment that was so different from the others. I therefore resolved that, if somebody entirely unacquainted with the circumstances of this experiment could point it out as quite ‘special’, then I could be justified in leaving out the results from further calculations. To conclude this instance, it may be added that after the erroneous, triple messing-up of its nest, the fish began a period of intensive nest-building, which is typical for fish that have lost their nest or have had it entirely destroyed.

Table 3. Experiment with disturbance of the nest. Nest-behaviour before compared with nest-behaviour after the disturbance of the nest.

Away from the nest

Fish no. and date	Bef. dist.		After dist.		vß	δ	u_o	u
	β_1	n_1	β_2	n_2				
R2 261 18/9-62	7.547	26	7.510	26	7.528	-0.037	-0.307	-0.536
R2 261 23/9-62	7.887	27	7.858	36	7.870	-0.029	-0.262	-0.511
R2 261 25/9-62	7.725	44	7.890	39	7.803	0.165	1.728	1.316
R2 C10 13/11-62	6.071	6	6.374	8	6.244	0.303	1.292	1.148
R2 231 15/11-62	7.500	31	7.465	33	7.482	-0.035	-0.322	-0.572
R2 231 16/11-62	7.482	28	7.298	23	7.399	-0.184	-1.506	-1.682
R2 231 22/11-62	7.610	34	7.852	46	7.749	0.242	2.464	2.020
R2 A10 22/11-62	7.394	26	7.326	26	7.360	-0.069	-0.573	-0.791
R2 C10 22/11-62	6.884	20	6.956	20	6.920	0.072	0.524	0.292
R2 A10 23/11-62	7.405	24	7.231	23	7.320	-0.174	-1.373	-1.551
R2 A10 28/11-62	6.758	15	6.915	16	6.839	0.157	1.006	0.789
Total	7.456	281	7.496	296	7.477	0.030	0.840	0.000

At the nest

Fish no. and date	β_1	n_1	β_2	n_2	vß	δ	u_o	u
R2 261 18/9-62	7.601	26	7.533	25	7.568	-0.068	-0.559	-0.430
R2 261 23/9-62	7.420	27	7.739	36	7.602	0.319	2.885	2.855
R2 261 25/9-62	8.214	44	7.810	38	8.027	-0.404	-4.201	-3.798
R2 C10 13/11-62	8.945	5	8.252	7	8.541	-0.693	-2.725	-2.646
R2 231 15/11-62	7.961	31	8.032	33	7.998	0.071	0.654	0.376
R2 231 16/11-62	7.767	27	7.714	23	7.743	-0.053	-0.430	-0.308
R2 231 22/11-62	8.031	35	8.074	46	8.055	0.043	0.441	0.542
R2 A10 22/11-62	7.910	27	8.133	26	8.019	0.223	1.869	1.895
R2 C10 22/11-62	8.725	20	8.890	20	8.807	0.165	1.201	1.255
R2 A10 23/11-62	7.705	24	7.997	23	7.848	0.292	2.304	2.316
R2 A10 28/11-62	8.722	14	8.044	16	8.360	-0.678	-4.266	-4.076
Total	7.989	280	7.977	293	7.983	-0.013	-0.367	-0.000

Table 3 contains the results of *Experiment 2*, ‘Experimental Disturbance of the nest’, where 11 series of observations were carried out. The *upper part* of the table concerns the results regarding initiation of nest-behaviour – that is, how long the male fish were away from their nests. The results written in the horizontal lines refer to the individual fish, whose numbers are lined up in the first vertical column. The lowest horizontal line, designated ‘total’, contains the results for all fish – which are marked ‘.’ in the text, say ‘ δ ’. β_1 listed in the second vertical column equals the logarithm (+10) to the parameter ω_1 , that has been estimated on the basis of observations from the time before the nest was messed-up. In the next vertical column, n_1 , one finds the number of occasions when each fish has been away from its nest during the same period. In the next two vertical columns the corresponding figures for the period after the nest was messed up are given. The following columns give $v\beta$ = the weighted average of β_1 and β_2 ; δ = the difference between β_2 and β_1 ; u_0 = the u -value from a test carried out with the hypothesis: $\delta = 0$ (the value being calculated from $\delta/M \sqrt{1/n_1 + 1/n_2}$; u = the u -value coming from a test with the hypothesis: $\delta = \delta$. (the value calculated from $\delta - \delta/M \sqrt{1/n_1 + 1/n_2 + 1/n}$). u_0 or $u = 1.96$ indicates (numerically) the 5% level of significance. – The test in the first case concerns the hypothesis that the fish are undisturbed by the experimental disturbance of their nests. – In the event of the hypothesis $u_0 = 0$ needing to be rejected, one may, with the other u , carry out tests to decide whether the individual δ 's relate themselves in such a way to δ . that it may be assumed that there will be a δ common to all fish. δ . may then be considered an estimate of this common δ . If one assumes that there is such a common δ , then one obtains the result that $\beta_1 + \delta = \beta_2$. This means that the parameter after the nest has been messed up can be written: ω_1 antilog δ . .

The digits in the lowest horizontal line entitled ‘total’ result from the following calculations: β_1 . = the weighted average of the individual fishes’ β_1 ; n_1 . = the sum of all n_1 ; β_2 . as with β_1 .; n_2 . as with n_1 .; $v\beta$. as with $v\beta$ equally; δ . = the weighted average of the individual δ 's; the ‘total’ u -values are calculated in the same way as the individual u 's.

The figures in the *lower part* of the table concern ‘behaviour at the nest’, and these have been calculated in quite the same way as those of the upper part just mentioned.

So, the results show, nevertheless, that a change in the nest’s appearance has no influence on the fish’s probability of initiating or interrupting nest-behaviour, but it is clear, on the other hand, that messing-up the nest brings about a change in the way in which the different forms of nest-behaviour occur. The quantity of fanning,

for example, has been clearly reduced, both because it is rarely initiated and because it lasts hardly a second if carried out, for no sooner do some loose parts of the nest begin to move, before the fish will stop fanning and start pushing instead. On the whole, the fish do much more pushing and both kinds of boring compared with the time they were at the nest after the disturbing intervention than before.

The difference may be seen in comparing the first and the second part of *Figure 3*. Thus the appearance or 'exposition' of the nest determines the kind of nest-behaviour that is carried out, but not how much is done - which means that the state of the nest is without influence on how the higher system occurs. Speaking aphoristically, it might be said that *what* the fish is doing is determined by the inner conditions of the fish, but *how* it is doing it is determined by the external conditions.

From the point of view taken up here it must be supposed that the fanning, which occurs in the part of the reproductive cycle of the stickleback investigated here, this 'sexual fanning' could be included under 'building' in Tinbergen's scheme. However, there are also other possibilities. Van Iersel (1953) distinguishes between '*parental fanning*' (that is, fanning that brings forward fresh water containing oxygen, when there are eggs in the nest - probably the phylogenetically oldest form of fanning and biologically the most important), and '*pre-parental fanning*' that starts to appear just before the end of nest-building, and expires when mating has taken place and there are eggs in the nest; after this 'parental fanning' begins. Sevenster (1961) divides 'pre-parental fanning' into '*courtship fanning*' (that occurs in alternation with real sexual behaviour or courtship behaviour - as happens when a male is presented with a ready female) and '*sexual fanning*' which occurs during the pre-parental phase when the male has not been presented with a female. Formerly, and from their biological fitness-point-of-view Tinbergen & van Iersel (1947), van Iersel (1953) and Sevenster (1961) had grouped 'sexual fanning' as a kind of 'care of offspring', which then appears as a displacement activity, caused by an unsatisfied sexual 'drive'. Personally I think there will be at work a proper, independent system for nest-behaviour - '*nest care*' - which may manifest itself differently during the whole reproductive

cycle. Through interplay with the other two systems, this ‘nest-care system’ could play an important role, together with factors in the environment, in determining how frequent the different forms of behaviour occur. To understand such system-interaction it is necessary to allow the higher-level ‘drive’-systems to express themselves through different forms of behaviour, which can be considered *synonymous* as the occurrence of one or another ‘behavioural synonym’ will be determined by specific, external stimuli.

Pre-parental fanning may then, more rightly, be divided into ‘*courtship fanning*’ and ‘*nest-care fanning*’, both of which are carried out with similar behaviour patterns, although stirred by either a ‘sexual drive’ or a ‘drive for nest care’. With these arguments I can therefore not confirm Sevenster’s idea, that pre-parental fanning is just a displacement activity resulting from a conflict with no obvious biological purpose, whereas ‘nest-care fanning’, according to our observations, has a definite, biological function – namely, that of ensuring that the nest is intact and well fastened to the substratum.

This issue is mentioned as an example to show that analyses of behaviour by means of statistical methods might lead to the discovery of hierarchical systems other than those arrived at alone by biological reasoning and methods.

The following two experiments were carried out to show how ‘pronities’ for activities at the nest can be influenced by various circumstances.

Experiment 3: ‘Creeping Through the Nest’

Mr. Finn O. Kapel, one of my assistants, carried out an experiment on some phenomena related to fanning. The results were used in connection with a project for an examination in 1960 but unfortunately never published, and the great number of publications on this topic from later years may now have eclipsed most of his results.

What particularly interested Kapel was how much fanning the individual fish performs, and how the fanning is distributed time-wise. He observed 58 male fish individually for 1 hour. In 4 of these observations the fish crept through their nests at moments that left at least 15 minutes of observation before and after this event. In

these 4 cases it was possible from Kapel's records - which have kindly been placed at the disposal for this investigation - to extract observations, which resemble those of *Experiment 2* with the experimental disturbance of the nest. The two experiments differ from one another only by the way in which the nest was disturbed, and by the fact that in one case the observation time was 30 minutes and, in the other, 15 minutes.

Table 4. Experiment where the fish creeps through the nest. Nest-behaviour before compared with nest-behaviour after the fish has crept through the nest.

Away from the nest

Fish no. and date	Before creeping through nest		After creeping through nest		$v\beta$	δ	u_o	u
	β_1	n_1	β_2	n_2				
92063 28/1	7.472	14	7.703	21	7.611	0.231	1.542	1.180
92063 4/2	7.433	15	7.635	21	7.551	0.202	1.376	1.023
90095 30/1	7.523	14	7.457	19	7.485	-0.066	-0.431	-0.595
91098 5/2	7.981	23	7.806	21	7.897	-0.175	-1.335	-1.401
Total	7.651	66	7.655	82	7.653	0.035	0.480	0.000

At the nest

Fish no. and date	β_1	n_1	β_2	n_2	$v\beta$	δ	u_o	u
92063 28/1	7.786	14	8.340	21	8.118	0.554	3.697	1.240
92063 4/2	7.926	15	8.361	20	8.175	0.435	2.932	0.529
90095 30/1	7.905	15	8.368	19	8.164	0.463	3.087	0.692
91098 5/2	7.996	23	8.030	21	8.012	0.034	0.259	-2.098
Total	7.916	67	8.271	81	8.111	0.348	4.827	0.000

The table gives the results of *Experiment 3* with time-measurements of the of the fish's behaviour before and after they crept through their nests. The explanation to the table is given in the legend to *Table 3*.

In the *upper* part of *Table 4*, which shows the time measurements for fish being away from their nests, there is nothing to indicate that the fish have changed by creeping though their nests:

All 4 individual u_0 's are below 1.96: 2 are positive and 2 negative (cp. the legend to *Table 3*). If one looks at all observations it seems that there are relatively few long intervals away from the nest during the first 10-15 observations after the fish has crept through the nest. This feature is, however, not clear enough to be taken into account here; but it may indicate the possibility that by observing many more fish for a longer period – or rather, on many more occasions away from the nest before they pass through it, and on fewer occasions after – then one would find that the fish is away from its nest for less time right after it has crept through it.

The *lower* part of *Table 4*, which give the time measurements for the fish staying at the nest, presents quite a different picture:

The first 3 fish have a large δ , just as $\bar{\delta}$ is large, and it proves that the corresponding u_0 is considerably larger than 1.96. The hypothesis $\beta_1 = \beta_2$ must therefore be rejected, both for the first 3 fish as for the whole of the material. So it may be investigated whether the individual δ 's are related to $\bar{\delta}$ in such a way that it would be imaginable that there is a common δ for which $\bar{\delta}$ is an estimation. The u -values for the test on the hypothesis that the individual $\delta = \bar{\delta}$ are less than 1.96 for the first 3 fishes, for which reason the hypothesis cannot be rejected for them. The u -value for the fourth fish is -2.098 and is thus (numerically) just above the level of significance.

If all information in the table is considered as a whole, then the most likely conclusion will be that the fish, with regard to staying at the nest, have changed by a factor which may be estimated as being 2.223 (antilog $\bar{\delta}$), which is to say, that on the whole the fish may be said to leave their nests about twice as fast, after having crept through them, as before they did it. If we consider the fish before it crept though the nest as a standard, its nest-behaviour after creeping through the nest may be described with the following formulae:

$$P\{t_f \geq T\} = e^{-\omega_{fi} \cdot \gamma_f^{(kR)} \cdot T^A}$$

and

$$P\{t_v \geq T\} = e^{-\omega_{vi} \cdot \gamma_v^{(kR)} \cdot T^A},$$

where the designations have the same significance as already indicated, except that ω_{fi} means the parameter of the individual fish for getting to the nest under the given circumstances, and to begin its behaviour at the nest - ω_{fi} is thus the parameter which is estimated for the individual fish 'being away from the nest', before it crept through it, and this parameter equals antilog $(\beta_1 - 10)$ in the upper part of *Table 4*; ω_{vi} is the parameter of the individual fish for staying at its nest, on the assumption that it has not recently crept through it; $\gamma_{fi}^{(kR)}$ and $\gamma_{vi}^{(kR)}$ are parameters common to all the fish,⁴ which state the effect of their having crept through the nest on the probability that they will leave the nest, respectively, the probability that they will come to it. As the behaviour, 'creeping though the nest', changes nothing in the probability of the fish coming back to the nest, then $\gamma_{fi}^{(kR)} = 1$ and, from a mathematical point of view, might be left out of the formula; it is, however, included here because of the psychological information it gives. (Similarly, parameters can be introduced in the general, theoretical formula for the effect of messing-up the nest in *Experiment 2*.)

If Fish no. 92063 4/2-60 is taken as an example, its behaviour after it has crept through the nest can be described by the following formulae:⁵

$$P\{t_v \geq T\} = e^{-0.00408 \cdot 1 \cdot T^{1.513}}$$

and

$$P\{t_r \geq T\} = e^{-0.00611 \cdot 2.22 \cdot T^{1.513}}.$$

Since the behaviour, 'creeping through the nest', only influences the probability of the duration of the behaviour at the nest, but not the probability of the duration of behaviour away from the nest, this is another confirmation of the fact that the two types or measures of behaviour vary independently.

4. In the parameters' indices 'i' stands for 'individual', 'f' (Danish 'fra') for 'from the nest', 'v' (Danish 'ved') for 'at the nest', and 'kR' (Danish 'krybe gennem reden') for 'creeping through the nest'.

5. As 'creeping through the nest' has no effect on the probability for beginning nest-behaviour the best estimate of ω_{fi} is antilog of the fish's $v\beta$.

In a broad outline, the changes in nest-behaviour do not differ much in this experiment from what was seen in *Experiment 2*, where the nest was disarranged with a small stick. In both cases, fanning disappeared practically after the disturbance of the nest, to be replaced by different forms of nest-behaviour, particularly pushing and boring.

Sevenster (1961, p. 60) found that the amount of fanning was limited right after the fish had been through their nests, just to increase afterwards to a certain level, before they passed through the nest again. He therefore designates the time that elapses between two episodes of 'creeping through the nest' as a 'fanning cycle'. The variation in the amount of fanning arises, according to Sevenster (*op.cit.*, p. 157), from a balance between a 'drive of aggression' and a 'sexual drive', and the occurrence of 'creeping through the nest' is due to a sudden shift from a large drive of aggression and a low sexual drive to the opposite.

The results of our *Experiment 2* and *3* can hardly be combined with this point of view. The amount of fanning does not change in a uniform manner in the two cases, while the total nest-activity is not affected by a disturbance of the nest.

Therefore it could be concluded that it was the nest's appearance that determined the amount of fanning and, when Sevenster found an increase in the occurrence of fanning per 5 minutes during the time after the fish had been through the nest, then the reason for this could be, that the nest was gradually put in order again. Nevertheless, the behaviour 'creeping through the nest' does bring about a change in the fish, but this change has to do with nest-behaviour in its totality - which is reduced, because the fish now remain for shorter periods of time at their nests every time they go there; this reduction must disappear again before the next 'creeping through the nest', otherwise one would have found a gradual fall in nest-behaviour during the total pre-parental phase. Sevenster's choice of name, 'fanning cycle' (*op.cit.*, p. 59), for such time periods is thus somewhat misleading, and another name like '*nest-care cycle*' might refer better to the observed phenomena.

If one takes the results of our experiments into consideration, and accepts the idea that a drive-system for nest care must exist, in

steady coordination with the drive-systems for aggression and sexual behaviour, then the conclusion will be easier to accept, that the observed drop in motivation brought about by the behaviour, 'creeping through the nest', can be traced back to this third system, thereby arriving at a plausible interpretation of our results.

The purpose of using measurement models in analysing complex psychological phenomena is to depict these phenomena as plainly as possible to facilitate the discovery of regularities. A fundamental requirement to the model is therefore that it can be interpreted and applied to the observation material in a realistic way. The following outlines an attempt to compare and coordinate our results regarding the behaviour, 'creeping through the nest', with results interpreted and explained by means other than those employed here.

Despite a great many investigations on the behaviour 'creeping through the nest' (especially by Nelson, 1965; Sevenster, 1961; Sevenster-Bol, 1962) the different aspects of this behaviour are far from straightforward. The lack of clarity is hardly due to insufficient knowledge of details but rather to a need for exact methods for comprising the various results into coherent expressions. Nelson (1965) makes a most interesting attempt at epitomizing our knowledge about the behaviour in different situations by means of a complicated model which, unfortunately, requires a number of ad hoc assumptions that seem to have been introduced in order to fit certain observations with the model – and not the other way round. Nor does he see the behaviour determined by various circumstances, for which reason no attempt is made at integrating forms of behaviour into systems, viewed as a whole and analyzed in detail. A reason for this may be that Nelson does not establish 'raw-scores', but notes behaviour per time unit. He is certainly right in being uncertain about Sevenster's (1961) and Sevenster-Bol's (1962) idea that 'creeping through the nest' is an *indicator* for a rather sudden shift in the balance between sexual and aggression-drives – but, as Nelson points out, one should perhaps take it the other way round: it is the occurrence of 'creeping through the nest' that *brings about* a change in the balance between the two drive-systems. This seems more evident if the behaviour in question is considered as a displacement activity – a kind of masturbation.

Basically, it is by 'creeping through the nest' that the male fertilizes the eggs laid in the nest by the female. But, as we have seen, the behaviour is also performed in situations without mating, and the behaviour in the two situations is similar. The first time the behaviour may be observed is after the males have completed their nests - with regard to size and appearance - and when they start reacting sexually, and not aggressively, towards ready females that enter their territories. Therefore the first 'creeping through the nest' is used to delimit the transition from the nest-building phase to the sexual phase. During the latter phase, the males are seen to pass through the nest with much varying intervals. The conjecture that the behaviour is a kind of masturbation could gain in credibility if there was an increasing probability for the male behaving with 'creeping through the nest' when presented with a female - even if she is shown locked-up in a test tube and therefore unable to follow the male to its nest. When the male passes through the nest, with a female present, it also happens that a small amount of sperm is excreted - which seldom happens to a male alone. Sperm excretion may also happen if eggs have been put experimentally into the nest before the male has been through it (Sevenster-Bol, 1962).

Still more surprising phenomena related to the behaviour, 'creeping through the nest', are described in Sevenster-Bol's 1962-investigations, which aimed at identifying the factors responsible for the diminution in sexuality following mating. Here it turned out that 'creeping through the nest' during mating had no decisive importance for any subsequent change of behaviour in the male. Nonetheless, it looked as if (1) the trembling behaviour - 'quivering' - which the male directed towards the female when in the nest, and (2) the presence of eggs in the nest, were important factors for the male's changing behaviour afterwards. A most unexpected result since 'creeping through the nest' and leaving sperm on the eggs must be considered the central behaviour for maintaining the idea of an autonomous drive-system for sexuality, and the first place to look for a drop in motivation. But as a matter of fact, this does not seem to be the case. So after having accommodated this surprising piece of evidence, it is perhaps no longer so exceptional to find an

increase in sexual tendencies and a decrease in aggressiveness after the periodical 'creeping through the nest' in isolated males.

However, as mentioned earlier, I do not think that all aspects of the behaviour, 'creeping through the nest', have been satisfactorily sorted out. Some clarity could be gained in following Sevenster-Bol's (*op.cit.*, p. 225) suggestion, that 'creeping through the nest' during mating consists of two behavioural components: firstly, 'passing through the nest', and secondly, ejaculation - corresponding to Larssons (1960) distinction between intromission and ejaculation in the mating behaviour of the rat. Having agreed on this idea, it seems to me reasonable to continue and consider the phenomena in a wider perspective. According to Larsson, intromission and ejaculation are just the very last parts of the male rat's mating behaviour, since they occur only after the male has mounted the female. However, in many species, mounting behaviour is also linked to dominance and aggressiveness, as perhaps first described in primates (Zuckerman, 1932). In this connection, and also in humans, it has been shown (Vanggaard, 1969) how certain forms of behaviour, which are almost impossible to distinguish behaviourally, may serve different social-psychological ends, no doubt because they belong to different bio-psychological systems with different dynamic backgrounds.

As mentioned above, something similar seems to be the case with the male stickleback's fanning-behaviour, the amount of which depends on (1) the state of the nest, (2) the presence of a ready female (who does not need to follow the male to its nest), or different conditions concerning eggs in the nest - that is, behaviour controlled partly by a nest-building system, partly by a sexual system, and partly by a system for care-of-offspring.

The behaviour 'creeping through the nest' can be viewed in a similar way. It occurs under the following four conditions:

(1) The male's first-time 'creeping through the nest', that marks the end of the nest-building phase and the beginning of the pre-parental phase - or the 'nest-care phase' and the 'sexual phase', as Sevenster-Bol (1962) calls them.

(2) That 'creeping through the nest', which the male carries out with variable intervals during the nest-care phase, and which is taken to mark the beginning and/or end of a nest-care cycle (cp. Sevensster's 'fanning-cycle', 1961).

(3) The 'creeping though the nest', which occurs when the male is presented with a female.

(4) That 'creeping though the nest', which the male performs during mating to fertilize the eggs.

By the *first two* variants of the behaviour, a shift sets in which brings about an increasing tendency in the male to react sexually, and a decreasing tendency to behave aggressively. Future research will show whether we may consider the first variant of 'creeping though the nest' as a special case of the second variant.

We are less informed about the *third* variant, and among the many results published about these phenomena I have not found a precise answer to the question, how the individual male stickleback changes after executing this 'creeping through the nest'. Nelson's (1965) observations of the behaviour just after the male has crept through the nest in the presence of a female, would seem to justify the conclusion that this also leads to an increase in sexuality but, as both factors contribute to the subsequent change of behaviour in the male, it is not possible to know how much of the change in behaviour is due to an after-effect of the sight of the female and how much to the 'creeping though the nest'. An estimate of our observations of the behaviour of males towards females before and after they had passed through the nest, *while* a female was shown, does not give reason to assume that 'creeping through the nest' enhances sexuality in the males and reduces their aggressiveness towards the females. The immediate impression from our experiments was rather the opposite - reduced sexuality and increased aggressiveness. So, for the time being, I dare say that the males do not change decisively regarding sexuality and aggressiveness after this variant of 'creeping through the nest' has been carried out.

With regard to the *fourth* variant of 'creeping through the nest', at present it is not possible either to say anything precisely about the effect of this behaviour, independent of other forms of behaviour that occur during mating. In comparing the different experiments of Sevenster-Bol (1962) I have, however, formed the opinion that this variant of 'creeping through the nest' is in all likelihood without greater influence on the balance between aggressiveness and sexuality - at any rate in relation to the effects of other occurring behaviours.

The available information on the effect of 'creeping through the nest' on nest-behaviour itself is also neither adequate nor precise. It appears from a great number of observations that the amount of nest-behaviour decreases considerably after the first 'creeping through the nest', but it is not quite clear how this decrease in nest-behaviour goes on. Does it mean, for example, that the fish spend less time at their nests than before, or that they stay away from the nest for longer periods, or a combination of the two (and if so, to what extent)? From our experiments it appears that the males, just after the *second* variant of 'creeping through the nest' spend considerably less total time at their nests. However, this happens alone because they stay for shorter periods at their nests, whereas this behaviour is without influence on the periods when the fish are away from their nests. Similarly, there is not much knowledge about how the *third* variant of 'creeping through the nest' influences the periods when the fish stay away from the nest; admittedly, there is much information about the different forms of nest-care behaviour, but as usual it is given in the form of the mean of behaviour patterns per time unit (1 or 5 minutes), and for variable numbers of fish; for this reason it is not possible to extract precise information about the duration of the periods when the fish are either at the nest or away from it. (See *Experiment 4*, below.)

Something similar must be said about the effects of the *fourth* variant of 'creeping through the nest'. And add to this, that during the mating(s) an important number of factors (the presence of eggs in the nest, etc.) must be taken into account. All this amounts to the fact, that these final conditions cannot be compared to the questions discussed here.

With this sparse information we can now round off our discussion of the two hypotheses on the behaviour of male sticklebacks during the pre-parental phase with the following hypothetical formulations:

(i) On the basis of the experiment carried out here, we can investigate whether there is an independent nest-care system – alongside with the assumed sexual- and aggression-system – and that ‘creeping though the nest’ brings about a decrease in nest-behaviour (the males are at their nests for shorter periods), after which sexual activity is easier and aggressive behaviour harder to release.

(ii) With the aim at testing Sevenster *et al.*'s assumptions of a two drive-system, a sexual- and an aggression-system, and that ‘creeping through the nest’ is brought about by a shift in the balance between the two (from a predominance of aggression to an ‘overweight’ of sexuality) – that is, to investigate whether the amount of nest-behaviour may be an expression of this change of balance.

We shall come back to these hypotheses when commenting on the next experiment.

Experiment 4: Presentation of a Female

4 male sticklebacks were observed for 15 minutes before they were presented for 5 minutes with a female ready for mating, but enclosed in a suitable glass that was put into the aquarium not far from the male. After the female had been removed, the male was observed again for 15 minutes. We thus obtained 3 sets of observations: (1) The behaviour of the male during the 15 minutes before the female was presented; (2) the behaviour of the male while the female was being shown, and (3) the behaviour of the male after removal of the female. Only the results of (1) and (3) shall be dealt with here.

Part (2) of this experiment with presentation of a female is among the 2 or 3 classical experiments with the rutting behaviour of male sticklebacks, and the procedure in parts (1) and (3), where the male is observed before and after the presentation of a female, has also been carried out many times. The only novelty in our experiment is thus the method of recording and processing the results and, as with the previous experiments, it is almost impossible to compare our data

with those of the literature regarding experiments carried out in recent years. For this reason no forms of behaviour shall be considered here other than the males' behaviour in relation to their nests and the effects on this behaviour from the presentation of the female.

Table 5. Experiment with presentation of a female.

Away from the nest

Fish no. and date	B. s. f		A. s. f		v β	δ	u _o	u
	β_1	n ₁	β_2	n ₂				
R2 231 29/11-62	7.680	18	8.170	30	7.986	0.490	3.784	0.315
R2 A10 5/12-62	7.096	11	7.694	19	7.475	0.598	3.634	0.863
R2 C10 11/12-62	7.616	18	7.995	26	7.840	0.379	2.846	-0.428
R2 261 12/12-62	7.659	22	8.000	15	7.797	0.341	2.345	-0.634
Total	7.564	69	7.991	90	7.805	0.443	6.276	0.000

At the nest

Fish no. and date	β_1	n ₁	A. s. f		v β	δ	u _o	u
			β_2	n ₂				
R2 231 29/11-62	7.999	19	8.159	29	8.096	0.160	1.248	2.405
R2 A10 5/12-62	8.623	10	7.993	18	8.218	-0.630	-3.678	-2.356
R2 C10 11/12-62	7.976	17	8.192	26	8.107	0.216	1.595	2.671
R2 261 12/12-62	8.223	22	7.420	15	7.897	-0.803	-5.522	-3.767
Total	8.157	68	8.009	88	8.074	-0.193	-2.705	0.000

The table gives the results of *Experiment 4* with time measurements of the behaviour of the fish before and after a female has been presented to them individually. *B.s.f*= Before seeing female; *A.s.f.* = After seeing female. Further explanation of the table is given in the legend to *Table 3*.

From *Table 5*, the *upper part*, it appears that, after the presentation of the female, the males have a higher tendency to start on nest-behaviour than before, as all males have a rather large δ . The results in the last column show additionally, that the fish seem to have changed in a manner alike, and that δ . is a good estimate of that change. Thus the male fish have increased their tendency to begin nest-behaviour with a factor 2.77 (= antilog δ).

The results in the *lower part* of the table regarding the conditions for 'remaining at the nest' are a lot more tangled. In the column showing δ , it appears that 2 males have a positive δ , whereas the other 2 males have rather large, negative δ 's. Furthermore, the negative δ . indicates that the males, considered as a group, have less of a tendency to leave the nest after seeing the female than before. The last column showing whether the males have changed in a uniform manner, corresponding to δ ., discloses that 2 males have changed more and 2 males less than δ . . There may be several possible explanations for these large individual variations. For example, that the female does not release sexual and aggressive behaviour to the same extent in all males, and that the two higher-level systems do not necessarily have the same influence on nest-behaviour. A reasonable hypothesis, and one that is easy to test, is to assume that males with a high tendency to leave the nest are stimulated by the sight of the female to prolong their stay at the nest later on, whereas males with an 'average' tendency to leave the nest do not change because they have seen a female. At any rate, such a hypothesis can explain the present result. However, there is one more factor of importance for the interpretation of the result - namely, that 3 of the males passed through the nest in connection with the presentation of the female (only Fish no. R2 A10 5/12-62 left that undone). Imagining that 'creeping through the nest' after the presence of a female has the same effect as the 'nest-care creeping through the nest' analyzed in the previous section, then we may resolve that the sight of the female has made up for the calming effect, which the behaviour of 'creeping through the nest' normally has - yes, in one case even been so strong as to have entirely cancelled out the effect of 'creeping through the nest'.

Now, attempting a conclusion in considering the group of fish as a whole, and ignoring the fact of the individual conditions of the fish, the most likely interpretation of the results is, that the tendency of the fish to leave the nest after having been presented with a ready female in 5 minutes has been changed with a factor of 0.641 (= anti-log -0.193). If 'creeping through the nest' works independently of the sight of a female - which it may very well do - then this estimate will not be quite large enough to account for the effect of a nearby

female, since it is calculated on the basis of results that include 3 fishes, which have crept through the nest, and thus have been influenced in the opposite direction of that coming from the female.

The large individual differences with regard to remaining at the nest may be explained by the possibility that the female releases sexual and aggressive behaviour in quite different proportions in the individual fish, and that the two drive-systems do not necessarily have the same effect on nest-behaviour. However, this can only be determined when more experiments have been done.

With these conclusions and assumptions the results indicate that the whole of the behaviour at the nest for males having seen a female, and having been through the nest, can be described by means of 6 parameters, which are included in the formulae:

$$P\{t_f \geq T\} = e^{-\omega_{fi} \cdot \gamma_f^{(kR)} \cdot \epsilon_f^{(sH)}} \cdot T^A$$

and

$$P\{t_v \geq T\} = e^{-\omega_{vi} \cdot \gamma_v^{(kR)} \cdot \epsilon_v^{(sH)}} \cdot T^A,$$

of which four parameters also formed part of the previous experiment while $\epsilon_f^{(sH)}$ and $\epsilon_v^{(sH)}$ signify the common parameters,⁶ which are due to the sight of the female and also concurrent for how long the individual male will stay away from or remain at the nest respectively. When the parameters for the effect of the sight of the female can be built into the formula without further ado, this is due to the fact that the two experimental parameters act multiplicatively, but separately, together with the fish's individual basis-parameter, wherefore all 3 parameters must interact multiplicatively. And it is worthy of note that it is possible to control this multiplicative relationship experimentally by comparing the fish that passed through the nest after having seen a female with other fish that did not do so.

Therefore, in this experiment we found that the activity at the nest markedly increased after the sight of a female, since both the probability of the fish leaving the nest, when they were at it, is small-

6. Concerning the parameters' indices, see p. 54, footnote 4. Further 'sH' (Danish 'se Hun') stands for 'seeing a female'.

er, and their probability of going to the nest when away from it, is greater. However, there seems to be no immediate connection between the changes in these probabilities.

As an example illustrative of the results of this experiment we may look at the behaviour of the male Fish no. R2 A10 5/12-62, who, after being presented with the female, did not pass through the nest. As mentioned, the sight of a female was calculated to influence the probability of leaving the nest with a factor of 0.641, but this value includes three fish who crept through their nests, thereby rendering the value opaque, since it is derived from *both* the effects of the exposure of the female *and* the effects of the males passing through the nest - just as in Nelson's (1967) experiment. Therefore Fish no. R2 A10, who did not go through the nest, may in fact illustrate the effects of seeing a female alone, if we use this fish's own δ for its behaviour at the nest. Supposing now that R2 A10, after having been shown the female, had passed through the nest and therefore was influenced by a factor corresponding to what was found in the preceding experiment, then we arrive at the following formulae for its behaviour:

$$P\{t_f \geq T\} = e^{-0.00125 \cdot 1 \cdot 2.77 \cdot T^{1.153}}$$

and

$$P\{t_v \geq T\} = e^{-0.0420 \cdot 2.22 \cdot 0.234 \cdot T^{1.153}} .$$

It will be seen that this way of working makes it possible to preserve information from previous experiments for use in the processing of results from new experiments. One may thus gradually arrive at a coherent understanding of *the joint coordination* of the different factors. In many psychological investigations there is, on the contrary, a tendency to gather more and more information about the effects of certain factors without leaving any clue as to how they work together. It was notably this lack of information about the connection between different results that led to the above problems of interpreting the conditions regarding the behaviour 'creeping through the nest'.

The lack of an entirely precise connection between different experimental results seems to me to be a fundamental trait of present-

day psychology that may be of decisive importance for its future development. For this shortcoming reveals itself in the lack of 'units' in psychology and confirms that psychology is, indeed, a 'young' science - however, not young in age, but in knowledge.

This is very well illustrated by the many different ways in which registration of observations and data-processing of results are carried out, and for this reason it has become increasingly difficult to compare results from different investigations of the same phenomena. A concrete example of such fundamental inaccuracy can be found in Nelson (1965) who otherwise, in comparison with many others, works most precisely, but nevertheless in some places notes observations as durations per minute, and in other places as frequency per minute - an incoherence which is bound to hamper integration of the many different registrations into a logical picture. (My own experiences with some dummy-experiments, where I committed a similar error, may also serve as a warning about this kind of situation.)

After the specification in this experiment of how the effects of different factors can be build into larger interconnected systems of formulae, we shall end by returning to the problem of the feasibility of working with 2 or 3 behavioural systems and their appertaining motivational factors.

There have been several reasons for working with two forms of motivation. *Firstly*, as mentioned above, van Iersel (1953) and others pointed out how the occurrence of different nest-behaviours could vary with the fish's incidental tendency to also manifest sexual or aggressive behaviour (an example in Sevenster, 1961, p. 58, shows that fish with much 'nest-care fanning' are also seen to react sexually in a rather strong fashion), just as forms of nest-care behaviour may alter the occurrence of sexual and aggressive behaviour (as when a male has just performed 'gluing' behaviour, a zigzag dance right after will rarely terminate with an attack on a passing species-member or a bite into an air bubble). *Secondly*, previous research has mainly ignored forms of stimulation for the experimental male animal other than presentation of a female, of another male, or of eggs in the nest. The influence of these kinds of stimulation has been

thoroughly discussed, whereas very few discussions have been devoted to the importance of the appearance or state of the nest and changes thereof (even in Sevenster's, 1961, p. 62, conclusions about the effects on the fish of its 'creeping through the nest' there is no mention at all of the state of the nest). *Thirdly*, due to the prevailing registration of behaviour per time-unit, little attention has been given to noting how the behaviour passes chronologically, or that certain forms of nest-behaviour may occur in series for example.

The assumption of a balance between two motivational systems, supposed to determine the different behavioural forms, may well explain the variations in nest-building that occurs even when the state of the nest is considered to be constant and unchanged. However, in a next instance it will be difficult to use the same balance to explain the fluctuations of behaviour that may be seen when the males are away from their nests – for example, when a male at one moment directs a zigzag dance towards air bubbles, snails, and the like, and at other moments launches a series of attacks on the same occurrences. Not to mention the increasing difficulties one encounters when the behaviour, 'creeping through the nest', enters the picture.

For although one may well appreciate that an ever-increasing excess-weight of aggression must finally result in a related behavioural synonym – say, 'creeping through the nest' – it will be difficult to use the same balance again to describe alternations between nest-care behaviour and no nest-care behaviour. And after that it appears even more difficult to employ variations in the same balance to describe the occurrence of different forms of behaviour when the male performs nest-care behaviour or does not care for the nest.

If, on the contrary, one adopts the idea of 3 kinds of motivating factors linked to: *a sexual system*, *an aggression system*, and *a nest-care system* – the latter being perhaps a variant of a 'care-of-offspring' system – then one will find it easier to explain the occurring fluctuations in behaviour by suggesting, say, that it is the balance between two of the not overtly active systems which, together with the stimulus situation, determines which forms of behaviour of the third system shall occur. Of course, this does not imply that the 3 systems should

be working in isolation on their higher level. Also, here we must calculate with interactions between the systems in such a way that it would be the strongest system which, at a given moment, and in one way or another, comes to behavioural expression. With this reflection, we are brought right back to the question touched upon in *Experiment 1* – namely, how do the higher-level systems balance themselves out and function during periods when they are not manifest in overt behaviour?

Our present scant knowledge does not invite us to proceed with this question by trying to account for the interaction between such higher-level systems, but it is nevertheless possible to point to precise ways in which the question might be answered. In fact it boils down to the problem of finding such a set of equations that may determine the occurrence of the different behavioural forms.

In case of the psychology of the stickleback, one could arrive at such equations through a sort of ‘marathon-experiment’ with a sufficient number of fish to allow all possible combinations to be observed closely. In making comparisons of both the probabilities for the activation of the higher-level systems and of the conditioned probabilities for the expressed forms of behaviour, one might arrive at a solution to the equation-system. With the comparisons made, as in the present experiments, a transfer of estimations from one part of the observations to another will render an increasingly complex and detailed specification of the probabilities of the behavioural forms. Since the fundamental principle here is *the comparison*, the ‘marathon-experiment’ could be divided into different series of experiments, if only they be done in such a way that each series contained an experiment identical with one from another series, so that their results could be built together in the same way as with what has been done here.

Should one finally wish to enlarge the possibilities of comparison, the ‘marathon-experiment’ could be extended with psychopharmacological experiments like those we carried out in order to test various compounds for minimising aggression in male sticklebacks for example. An interesting result of such pharmacologically induced changes of motivation show that the territorial defence may disappear completely, as well as the numerous attacks on pass-

ing females, whereas nest-care behaviour do not change in a way that correspond to the disappearance of aggressiveness - which does not speak in favour of the assumption of an aggression-system as one of the only two dominating systems. In several places, van den Assem (1967) gives some consideration to the relation between nest-building behaviour and aggression, as he finds nest-building to be inhibited by increased aggressiveness. His position regarding the question whether there are 1 or 2 motivating systems, is, however, not very clear - for if nest-building and aggressiveness depend on the same kind of motivation, then this very motivation may be 'used up' since too much 'energy' goes to aggressive behaviour away from the nest, leaving very little 'energy' for nest-building. A first rough impression from the mentioned psycho-pharmacological experiments points rather to the possibility of 2 partly independent systems, but only further experiments may help to clear up the matter. Whatever it will be, the experimental possibility of including psycho-pharmacological changes of motivations to enlarge our 'equation-system' is just one way to improve on the estimation of the different active factors and their integration with other factors in the systems.

Should a third system exist, which our results indicate, then the behaviour, 'creeping through the nest', may be considered as one of the forms of behaviour that is capable of reducing the higher-level system in such a way that nest-care behaviour will be declining in expression, since the males spend less and less time at the nest, and also that this reduction brings about a simultaneous change in the 'balance of the systems' when they do not come to behavioural expression.

11. Summary and Discussion of the Results

As will have emerged from the preceding account, the project under consideration is, to a great extent, organized like a Chinese nest of boxes, in so far as every step taken to carry out the experiments as related has had its source in a definite problem belonging to a larger complex of problems of human psychology. Some questions of detail found their answers *en route*, more or less satisfactory as reported

in the experimental part, but the experiments also yielded additional results that now enable us to enlighten the original general problem.

However, before that, the results directly related to stickleback behaviour merit, after all, a general comment. The original starting point was to experimentally investigate certain 'primitive reactions' found in humans (pilot-aspirant's symptoms and Braatøy's observations) by means of simple animal experiments. The first of these were about the reactions of male sticklebacks to the introduction of a specific stimulus (a dummy), which, despite its apparent simplicity, turned out to be too complex a situation for arriving at an exact evaluation of the results. Therefore, an even simpler situation was chosen for observing the behaviour of isolated male sticklebacks and the effects on them of some reasonable limited interventions. But also in this situation, the occurrence of the different behaviours appeared to be so complicated that the processing of the results had to be given up in the first instance. It seemed to be necessary first to carry out analyses of the occurrence of whole, assembled behavioural systems, always assuming that the symptoms and 'primitive reactions' we originally wanted to study did indeed correspond to the different forms of behaviour in our experimental animals, and not to the higher-level motivational systems behind the overt behaviour. With this in mind, it must be concluded that we have not obtained much concrete knowledge about the phenomena we originally set out to investigate. Nevertheless, I am of the conviction that we have come to know a good deal about methods that can be used to study the many different behavioural forms in animals and humans, as well as their theoretical implications of a more general nature.

In continuation of this, we shall now have a closer look at the above formulae for the behaviour description, in order to see what their parameters really represent.

The Different Parameters

In the formulae that describe the behaviour of the fish, there are actually parameters of different nature. Whereas ω varies from one

individual to the next, $\gamma^{(kR)}$ and $\epsilon^{(sH)}$ are parameters common to all fish, and they are furthermore what Rasch (1966) has called 'specific objective' (*i.e.* the parameters are estimated in such a way that their value is independent of the particular individual that has been observed). This is not occasion to account for this fundamental concept – here it suffices to point out that $\gamma^{(kR)}$ and $\epsilon^{(sH)}$ only dependent on the circumstances they describe (respectively the effect of the male passing through the nest, or having seen a female), while they are independent from all the other factors which determine the behaviour of the male fish in the given circumstances, and which are common to the two compared situations of observation. This may, for example, be seen from the fact that the two parameters state how the original ω of a fish *changes with* the experimental intervention, and consequently, beyond that, says nothing about the tendency of a fish to stay at its nest. Thereby the content of $\gamma^{(kR)}$ and $\epsilon^{(sH)}$ is made as exact as it is possible to describe the experimental intervention but, on the other hand, it becomes independent from the remaining, less precisely described, experimental conditions which are common to both situations. Another advantage of parameters of this kind must be seen in connection with the biological experience that, while '*absolute levels and ranges of variation may easily happen to change with the environment, the relations between two or more variables with a common basis are more stable*' (Rasch, 1966, p. 2).

In contrast to this exact content stands ω , which depends partly on a good many factors in the individual fish, and partly on a great many factors in its environment. The ω determined for each fish is thus a function of each of these sets of factors, and therefore it might be tempting to divide ω into two quantities: one which characterizes the individual fish and another characterizing the milieu of the fish before an experimental factor is introduced. To do this, however, we do not have a similar basis or standard of comparison as we had for the evaluation of the other parameters, where it is possible, say, to compare the behaviour before and after a fish has crept through the nest.

For such a comparison actually implies an order of precedence with regard to which situation is yielding the largest probability for having the behaviour at the nest interrupted. If a certain base-situa-

tion is used as a standard, we may in this way determine how a given experimental intervention changes the conditions and indicate the relation between the situations before and after the intervention. In fact, employing such an order of precedence does not really differ much from what is done, for instance, when one measures objects with a measuring rod – also there it may be said that the objects are put into a system of precedence according to size in relation to a standard, for example the defined meter. Therefore $\gamma^{(KR)}$ and $\epsilon^{(SH)}$ may be said to be *a measure* in a stricter sense than most other psychological measures which, in a certain sense, are only registrations.

Narrowing Down Individual and Milieu Parameters

Should we wish to divide ω into one parameter of the individual and another of the milieu, we would realize that it is not possible to make such a comparison of two situations alike. For if we tried to compare the behaviour of the same fish in two aquaria in order to determine the milieu parameter, the fish would have changed so much by being moved into another tank, and after having built a new nest, that, from a psychological point of view, one could not talk about 'the same' fish in the two situations. Similarly, if we wished to determine the individual parameter by comparing, one after the other, the behaviour of two sticklebacks in the same tank (*i.e.* in the territory of Fish no. 1), then Fish no. 2 would build its nest right away and thereby create a new milieu in the aquarium. Thus, experimentally, we cannot find two situations to compare in which either the fish, or the milieu, have been changed separately. But we may nevertheless compare and measure the individual fish with regard to their deviation from a standard. If it could be assumed that conditions between one aquarium to another were alike, the variations in behaviour of the fish would only arise from individual variations between them, and the parameter stating the deviations from the standard would thus be a quantity that really characterized each *individual*. Although we aimed at making the conditions as uniform as possible from one tank to another (a detailed description of aquaria and fish is given in the dissertation, ed.), there will inevitably be certain variations between the aquaria,

not least with regard to factors whose influence is not yet known. The parameter stating the measure in relation to a standard will thus depend – at any rate from a strict theoretical point of view – both on factors that characterize *each individual* and *each aquarium*. Thus it will not, in terms of prevalent psychology, be a ‘pure’ individual parameter, but a parameter for a given individual with regard to a given type of behaviour in a given situation. It is possible that this is *a necessary epistemological consequence of the impossibility of assessing an individual without doing it by means of its behaviour in certain environments*. As psychology has not yet found its firm, basic concepts or a yardstick for them, such a realization is bound to carry a certain, important weight.

However, in practice this uncertainty regarding the individual parameter will decrease, the better we understand the factors that determine the behaviour: the more factors of the milieu that can carefully be described and controlled, the more it will be possible to make the individual parameter independent of factors in the milieu – and the more of the individual-dependent factors, which can be mastered in a similar way, the less individual variation we may suppose to find between the individual fish. A closer analysis of the individual parameter could also enlighten the above discussion, whether there would be 2 or 3 higher-level systems according to which the behaviour of the sticklebacks were to be systematized. We can well imagine that ω could be made up of 2 or 3 main units: alone, the number of hormones (androgen, adrenaline, prolactin, etc.), supposedly exerting an influence on the behaviour, implies that ω can be split up into many independent components. The way one will come to consider the behaviour – as grouped into 2 or 3 systems – may no doubt depend on how ω can be split up most appropriately; but the choice of either a two- or three-system point of view will be of great importance presently for how the probabilities of the occurrence of the different behavioural forms are going to be considered. But a division of ω into a number of system-units or components does not free us from the problem mentioned on p. 30, that there may be so many important factors that it will be utopian to imagine that variations in the individual parameter should ever

disappear completely, as it might very well be impossible to master all factors at the same time.

Rasch's analyses of the outcome of intelligence tests (Rasch, 1960) dealt precisely with such well known psychological phenomena that it was possible to control the most important factors of the milieu – such as the room in which the tests were carried out – to such a degree that their effect could be said to be without importance for the psychological phenomena under study. So in a certain sense, the personal parameters, estimated in Rasch's investigations, may be said to be 'pure' individual parameters. The same cannot be said about the individual parameters in our investigations of sticklebacks or the outcome of testing more complicated traits of personality (for instance by the current personality tests of psychology), since we know too little about the chief influencing factors, and how they are to be brought under control.

But even so, if the object is to estimate the individual parameter by means of a standard, which standard should we then choose for the assessment of the individual fish? Since it is a question of a measurement, we have a rather free hand for choosing a standard – as when others have chosen units of measurement in many other sciences. Spontaneously one might feel attracted by choosing the mean as a standard, that is, the average value of the parameters of many fish. So fish with a high tendency to leave the nest would get an individual parameter above 1, and the others would get parameters below 1 – at any rate as long as the conditions common to all tanks remained unchanged. At present, however, there is nothing to indicate that this will be important information to obtain about the individual fish and, as the experiments which have given information about the mean cannot be reproduced with exactness – the fish have died long ago and the tanks have since been altered many times – there is not much that speaks in favour of choosing such an occasional average, for it would not be a scale that could be taken up again and again and used as required.

On the other hand, there is something to indicate that fish, which have both an unusually feeble tendency to start on nest-behaviour and a particularly high tendency to leave the nest on the whole, follow a set of laws that differ from those of the others. In order to

distinguish these two groups with ease it has turned out expedient to let the standard have the parameter $\sigma_f = 0.00125$ for going to the nest, and the parameter $\sigma_v = 0.0250$ for staying at the nest; groups of fish with rather insignificant nest-behaviour will then get the individual parameters $v_f < 1$ and $v_v > 1$, whereas fish with more normal nest-behaviour get $v_f > 1$ and $v_v < 1$. (Cp. p. 38, above, and please note that $\sigma_f = 0.00125$ gives $\log \sigma_f + 10 = 7.0969$, and that $\sigma_v = 0.0250$ gives $\log \sigma_v + 10 = 8.3979$.) Looking now at the fish that was used as an example in *Experiment 3* we find that its $\omega_f = 0.00408$ and split-up into $\sigma_f = 0.00125$ and $v_f = 3.26$ (as $0.00125 \cdot 3.26 = 0.00408$), and that its $\omega_v = 0.00611$, split-up into $\sigma_v = 0.0250$ and $v_v = 0.244$.

The value of calculating an individual parameter for each individual fish may be a little problematic. However, in my experience it has the practical value, that it is easier to evaluate the state of the individual animals, and thereby to determine regularities that are valid only for special groups. The individual parameter has also been introduced here mainly with a view to its practical side, namely in order to show that *it can be estimated*, and to draw attention to the methodological problems which the individual parameter may give rise to.

It is now possible to describe the quantity - not the art or quality - of a male stickleback's nest-behaviour with the help of the theoretical formulae:

$$P\{t_f \geq T\} = e^{-\sigma_f \cdot v_f \cdot \mu_f^{(rR)} \cdot \gamma_f^{(kR)} \cdot \epsilon_f^{(sH)} \cdot T^A}$$

and

$$P\{t_v \geq T\} = e^{-\sigma_v \cdot v_v \cdot \mu_v^{(rR)} \cdot \gamma_v^{(kR)} \cdot \epsilon_v^{(sH)} \cdot T^A}$$

The first formula gives the probability that the fish will continue to be away from its nest **T** seconds after having left it last time, while the other formula states the probability that the fish is still at its nest **T** seconds after having arrived there last time. The parameters of the formulae refer to the factors worked with above, and whose significance and mode of operation have been determined. On the other hand, the formulae do not express anything to indicate that all factors may exert their influence simultaneously in the same ex-

perimental situation (thus it would be without meaning to mess-up a nest immediately after the male fish has been through it). σ_f and σ_v give the probability of the standard fish for respectively arriving at or leaving the nest in the standard-situation; by definition the values of them have been put at 0.00125 and 0.025 respectively. v_{fi} and v_{vi} denote the individual parameters of the fish - in relation to the standard fish - for going to the nest or remaining away from it; it goes without saying that the values of these parameters vary between the individual fish. $\mu_f^{(rR)}$ and $\mu_v^{(rR)}$ give the effect of an experimental disturbance of the nest that is common to all male fish, which are both equal to 1 (meaning then, that this experimental operation is without influence on the *total amount* of nest-behaviour). $\gamma_f^{(kR)}$ and $\gamma_v^{(kR)}$ denote the effect of a male fish creeping through the nest - an effect varying according to how the fish change as a consequence of their staying at or away from their nests, but an effect common to all male fish regarding the two conditions; this factor has the respective values of 1 and 2.22 (signifying then, that the fish are unaltered a long time away from the nest, but leave it considerably faster after having crept through it). $\epsilon_f^{(sH)}$ and $\epsilon_v^{(sH)}$ give the effect of the sight of a ready female, an effect common to all male fish, but different with respect to the behaviour at the nest and away from the nest, with the values of 2.77 and 0.234 respectively (which means that the fish are much shorter away from and much longer at the nest, implying that, on the whole, there is much more nest-behaviour after the sight of a female).

A is an immensely general quantity, as it is a constant common to all fish in all situations investigated here. It applies to the formulae, which describe the behaviour at the nest and away from the nest, despite the fact that the quantity of behaviour away from the nest varies independently from the quantity of behaviour at the nest. In addition, A also seems to apply to the first detailed behavioural form, 'creeping through the nest', the occurrence of which we have started to study. Furthermore, it applies to observations made in one year in one room by one observer (*Experiment 3*) as well as in another year in another room by another observer (the remaining experiments). Since A is common to all series of observations un-

dertaken here, it cannot really be considered as a proper parameter, but must be regarded as an empirically determined constant, about whose content it may be too early to try to guess. Because **A** has such an importance for the occurrence of the behaviour, it may be just to connect it with the above mentioned (p. 18-20) 'displacement-movements', which occur in situations where the milieu permits only a very slight probability for their occurrence right after the behaviour came to an end last time. Here the magnitude of **A** could be of great importance, if it should turn out to vary from one behavioural system to the next, or between one animal species and another. In this connection it is therefore important to underline, that **A** is only determined here for one animal species with respect to its nest-behaviour.

The values of the present estimations will, of course, be important only to those especially interested in the behaviour of sticklebacks. It may, however, be of far more general interest that it has been possible, *firstly*, to estimate them at all. *Secondly*, that each parameter may be delimited in such a way that it only depends upon one single definable and controllable factor, while the many other factors that influence nest-behaviour are without influence on the different estimations; for example, the estimation of the parameters, indicating the effect of the fish 'creeping through their nests' does not depend on how big their nest-care drive happens to be otherwise; the parameters for the effect of 'creeping through the nest' are common to all male fish, whether they have much or little nest-behaviour. *Thirdly*, that it has been possible to determine how these many factors work together. Thus the experience of working with these experiments suggests that it is, indeed, possible to build up an extensive formula, which, in the course of time, comes to include all factors whose effects may be determined little by little. In this way we may obtain a more and more comprehensive and coherent understanding of the system and of how the individual factors influence behaviour.

The work so far concerns only factors that exert influence on nest-behaviour in fish during their rut, when they have built a nest and thus have a considerable nest-activity, but one may also use the same methods for studying factors that determine nest-behaviour

and, say, measure the influence of various doses of hormones on castrated fish.

Until the present time, there has been a tendency in psychology to register the effect of now one factor by means of one population, and now another factor with another population, for which reason it has not been possible to get an idea of the mutual relationship between such factors. This has, however, been brought about here. Of course, it is not very probable that, in further research of this kind, one shall find factors interacting in a similar simple fashion, where they have all acted multiplicatively, but this is not a necessary condition for using the method, even though it makes the work a lot easier. (An example of factors interacting in other ways is found in Reventlow, 1970, pp. 132-33; ed.)

What a Measurement Model May Require of the Psychological Phenomena

As mentioned on p. 29 there has to be a certain correspondence between what is observed and the model used to describe the observations. We can now go the opposite way and say something about how the psychological phenomena must behave in order to be described by the model now arrived at.

It has already been discussed (p. 40) that there is an increasing probability for an interruption of a behaviour depending on how long it has lasted. This is why **A** was introduced. However, there is more in the formula than that. In many psychological theories it is suggested that some kind of 'drive-reduction' or 'need-satisfaction' is taking place while the behaviour is being carried out, after which the 'motivation' is supposed to have been 'used up', as it were, bringing the behaviour to end. However, the state of motivation will increase again and in due course attain a sufficient level or strength thereby reproducing the behaviour. Obviously, the idea is that *a change* occurs in the individual when the behaviour is being carried out. Regrettably it is not possible to pursue this rather complicated problem in detail, even though it might be elucidated in many ways by our observations regarding nest-behaviour - among which, on second thoughts, a few points deserve attention.

Nest-behaviour has turned out to be describable by means of a set of constants that necessitates no assumptions about motivational changes in the individual as some behaviour is going on. On the other hand, the probability function may also refer to processes in the individual, and then the constants will say something about the rate of speed of the processes. (One can think of a water tank with small holes in the bottom; the probability formula may then be likened to a formula for the water level, and the constants to the sizes of the holes.) On that ground one may claim that the individual changes. Referring to the above discussion of 'need-satisfaction', it may be expected - at least as a spontaneous guess - that, as **A** (with its value of 1.513) in the formula implies an increasing probability of the cessation of behaviour, the behaviour might bring about a change in the state of motivation. However, this would be a misunderstanding, for several reasons: (1) Since **A** is common for so many different observation situations, it would appear strange for it to be an expression of both an increase and a decrease in the motivational state. Neither does it agree with general experience that a state of motivation increases and decreases with equal speed in all individuals in all situations - not even with reference to the same behavioural system; (2) According to our preliminary experience, **A** may also enter the description of the initiation and interruption of fanning-behaviour - and it does not seem immediately understandable why a *subsidiary* state of motivation - always assuming that it can only exist if a higher-level system 'is on' and functioning - should be satisfied and then increase again with the same speed as the higher-level system which, remember, may also reveal itself in many other behavioural forms in the same individual; (3) Supposing that **A** could be an expression of a sort of 'need-satisfaction', then it would also have been quite understandable, if there had been an additional connection between the stickleback's 'remaining at the nest' and 'being away from the nest', and not, as we have found, that these two forms of behaviour vary independently from each other.

A much clearer impression of 'need-satisfaction' can be obtained from *Experiment 3*, where the fish's 'creeping through the nest', sup-

posedly implying masturbation, brings about a far greater tendency for the fish to leave the nest.

Problems about phenomena of motivation, and the reduction of motivation through 'need-satisfaction', may also be elucidated in another way with the help of the proposed description models. For the sake of clarity, here we will stick to the simpler model we originally tried to use, where

$$P \{t \geq T\} = e^{-\lambda T}, \quad (1)$$

which in principle is of the same type as the model we ended up using. Still, we found it necessary to use two versions of the model in order to describe nest-behaviour satisfactorily - namely, one model that describes the tendency of the fish to initiate nest-behaviour (*i.e.* something which may describe motivation in one or another sense), and another model for the tendency of the fish to stop performing nest-behaviour (*i.e.* something that may describe a kind of 'need-satisfaction'). Attention was brought to the surprising fact, that there was no correlation between the parameters in the two versions of the formula.

As emerged from the analysis of the content of the formula (p. 33f., above), λ is the only parameter that gives information about psychological matters, but it was also pointed out how λ could enter differently into different mathematical expressions in unlike manner, which were in fact only different versions of the same relations.

This is of great importance for arriving at a definition of motivation, and in order to put forward laws about motivation based on observations. For if our formula should happen to say something important about motivation, then - depending on how one registers the observations - one will reach conclusions deviating so much from one another that it is tempting to believe that they reflect disparate regularities.

To illustrate such a situation, let us imagine three researchers who wish to know something about nest-care motivation in sticklebacks in the form of the fishes' tendency to begin their nest-care behaviour. To simplify things, let us assume that it is possible to describe

the researchers' sticklebacks with the same λ regarding this behavioural tendency.

The *first* researcher observes the time lapse between the moment the fish leave their nests and the moment they return and resume nest care. This researcher will find, as time passes, that there are fewer and fewer fish starting on nest-care behaviour, which leaves him with the impression that there is a drastic difference between the majority of the fish, as they perform nest-behaviour, and a few of the remaining fish that have a very feeble inclination to do so (as in the aforementioned case of a fish which, with a certain λ , is observed now to be less than 10 seconds away from the nest and now several hundred seconds away from it). So, what our first researcher observes here is how the psychological parameter λ manifests itself in the above formula (1).

The *second* researcher has chosen to register how many fish start their nest-behaviour within certain short time intervals. He will find that, although there is a difference between the number of fish that initiate nest behaviour within the different short time intervals, this very difference is just an expression of a gradually decreasing tendency. For, in fact, this researcher is observing how λ works in the following formula

$$P\{T \leq t < T + 1\} \approx \lambda \cdot e^{-\lambda T}.$$

The *third* researcher may be supposed to register how many per cent of those fish that have not yet started on nest behaviour, will begin performing it during a given time interval, and he is likely to find that this percentage is constant - namely λ .

However, further contemplation on the nature of their registration methods, and their bases, will disclose that, in reality, they have all been dealing with the same psychological phenomena, namely that of homologous behaviour by homogenous animals in uniform environments. This illustration is just a renewed discussion of the apparent contradiction, which appears when one is asserting, on the one hand, that a fish's probability for continuing a behaviour once initiated will be lower and lower, and, on the other hand, maintaining that the same fish's probability for interrupting the behaviour is constant.

It is obvious that it will lead to serious misunderstandings, if these forms of descriptions of motivation are confounded. It should also be added, perhaps, that there may not either be any connection with the satisfaction of a need, which can be felt as one carries out, or has carried out, some kind of behaviour, and what is expressed here mathematically in the formulae.

It goes without saying that the psychological interpretation of the mathematical expressions depends on which specific expression one has chosen to consider. Much confusion about *the concept of need* may have emanated from differences in methodology, when, say, one researcher with his special observation-methods had been dealing with phenomena that showed up in one particular mathematical expression, whereas other researchers meant to occupy themselves with phenomena that turned up in some other mathematical expressions, as in our illustration above.

As a final conclusion derivable from the experiments, some interesting information about the relation between individual and milieu should be mentioned. *Experiment 2* showed that a certain change of the stimulus situation (messing-up the nest) was without influence on the amount of the total nest-behaviour, but had a decisive influence on which of the behavioural system's various forms were carried out. *Experiment 4* showed just as clearly that a certain stimulus-situation could change - increase - the amount of nest-behaviour. As the effect was clear, even after the stimulus had been removed, it must be said that it has changed the fish's condition. There is thus a significant difference in the way the two stimuli work in the two situations. As is the case with need-satisfaction, it is also of a decisive importance here that the effect of the milieu on the higher-level system is not confused with the effect of the milieu on the individual forms of nest-behaviour.

12. The Initial Conditions of the Investigation Enlightened by Its Results

In conclusion we shall briefly return to the psychological starting point of our experiments. To support the evaluation of results it will

not be amiss to reconsider the a priori assumptions that were the premises for employing a probability model on the behaviour of sticklebacks.

ad Assumption I: The obtained results will hopefully have testified to the reasonableness of the first assumption (see p. 31), that by observing durations it is possible to get relevant information about certain psychological aspects of the nest-behaviour of male sticklebacks.

ad Assumption II: As argued (pp. 32, 36f. and 40), the second assumption had to be rejected but could be replaced by an empirically strengthened conjecture that the probability of a fish leaving its nest (compared with arriving at the nest) increases potentially with a constant factor.

ad Assumption III: The situation regarding the third assumption, that the durations of the different forms of behaviour are stochastically independent, is more complicated to assess. Stochastic independence implies *inter alia* that a fish must not change behaviour in a certain direction during the observation period and, due to learning for example, stay longer at its nest each time it goes there. However, in the experiments under consideration here, processes of learning are practically absent, which is the reason why the individual fish may be considered 'constant' in this respect. In other respects it is far from certain that they remain 'constant' during the observation period.

From *Experiments 2 and 3* it emerged that the behaviour changes both after 'messing-up of the nest' and 'creeping through the nest', in that the fish were seen to employ different behavioural forms to bring the nest in order again. Thus, after disturbing the nest, more fanning is performed in tempo with repairing the nest, in which pushing, boring and gluing may occur - after which the occurrence of these latter forms will gradually drop, wherefore the appearance of the different behavioural forms cannot, strictly speaking, be considered stochastically independent. However, as repairing a nest is a gradual process, the fish can only be considered 'constant' regard-

ing the execution of the different forms of behaviour for limited periods of time.

If, on the lower level of the hierarchy, the transition from one kind of detailed behaviour to another should influence the quantity of behaviour on the higher level – which is investigated here using the collected amount of nest-behaviour – then this change should also show up in the comparison of the behaviour before and after the nest has been ‘messed up’. However, such a change is not seen in this experiment, and for this reason we must conclude that the appearance, or exposition, of the nest is without influence on the amount of – the durations of the total – nest behaviour. Neither are there reasons to believe that the gradual return to the behaviour, which the fish had before ‘messaging-up the nest’, should give a systematic change in the durations of the fish being at or away from their nests. Nor is there any systematic change in the detailed forms of behaviour as such, which all together amount to not rejecting the assumption of stochastic independence with respect to these observation periods.

In *Experiments 3 and 4*, where the male fish crept through their nests, respectively, and were presented with a female, the durations of their staying at or being away from the nest did change after the experimental interventions. In both cases the fish returned to their original behaviour after some time. But since the effects of the interventions last longer than the observation period, and no clear systematic change in the durations of the behavioural forms is seen during the observation periods, it seems justified also in this case to accept the third a priori assumption, that there is stochastic independence between the durations of the different forms of behaviour during observation periods of the length used here.

13. Final Remarks on Methods for Studying Motivational Systems

A line further back should finally be drawn to the test-psychological problems and the syndromes of pilot aspirants and psychiatric patients. Here part of the difficulties in making comparisons between the results of various personality tests resembles those we encoun-

tered when comparing different descriptions of stickleback behaviour. For not only does one and the same psychological system manifest itself to a varying degree from one test to the next, and from one person to the other, but the system may also come to expression in quite different ways under different circumstances.

It might therefore be desirable to subdivide the observed behaviour into parts, which are both recognizable from one situation to the next, and constituted in such a way that some parts may characterize the individual and some the stimulus situation in question (cp. p. 15 and 41). Now there is, however, much to indicate that the different forms of behaviour originate from a joint action of the individual and the stimulus situation, and that, consequently, it is not possible to get as simple a division as the one just suggested (see results of *Experiment 2*). The matter can, however, be reformulated by saying that the occurrence of very different behavioural forms may mean that one and the same higher-level, psychological system has been activated in such a way that these different behaviours can be considered 'synonymous'. The task will therefore be *to analyse the behaviour collected into such 'synonyms' that may then be integrated into units with a certain shared content*. One may then analyse how the different 'synonyms' respectively vary from one person to the next, and from one situation to another. It is, of course, to a certain degree what is done when one constructs a test battery, but it is rarely done on the basis of really thorough analyses like the ethologists, for instance, are seen to be doing in their studies. Thus there are not many human forms of behaviour that have been described in as much detail as, for example, the nest-behaviour of the stickleback.

It is obvious that no direct information can be obtained as to how emotional systems appear in human beings in test-situations from experiments on nest-behaviour in sticklebacks. The best one can hope for is to get some general knowledge of the systems, which may enlighten observations made on humans in test-situations. The present investigations seem to me to have met such expectations to a certain extent, partly due to the form of methods for the description and investigation of emotional behaviour to which they have led, partly due to the information they have given about how individual and milieu factors act together in emotional systems.

In a test-situation a milieu is set up which particularly activates those systems that form the purpose of the evaluation (we also know such milieus from the sticklebacks, for instance when a female on heat is shown to a male; such experiments have indirectly been touched upon in *Experiment 4*, where only the after-effects of the stimulation were considered). If behaviour in a test-situation may say anything of value for behaviour outside the test-situation it must imply that the amount of behaviour is influenced in such a way that it is only attributable to the test, whereas the factors characteristic of the individual outside the test situation, remain uninfluenced. If the order of precedence with regard to the system examined, which is valid for individuals outside the test-situation, undergoes a change due to the test, then the prognosis, which the test may bring about for behaviour outside the test situation, will become very uncertain. Therefore certain general regularities for the occurrence of the system have to be the same both inside and outside the test-situation.

Even though, as already mentioned, the experiments with sticklebacks do not resemble real test-situations (none of the situations observed are particularly provoking), we may nevertheless rightly assume that the regularities established here may well throw light upon certain important conditions in test-situations with humans.

Among such regularities, one may point to the importance of:

- (1) a distinction between how often a system occurs, and how long it remains activated;
- (2) that one and the same system may manifest itself in various ways under different stimulus situations.

The difference between two tests that both give information about a system, of the kind in which we have been interested, will therefore be revealed by the degree to which they may provoke the system to be activated and, respectively, how long they let the system remain activated, and also with regard to which of the system's potential ways of manifestation they may be provoking.

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A Commentary by Jens Mammen (1986): On Mathematics and Psychology

Or Notes on Mathematics, Intuition, and Reality
(inter alia sticklebacks)

The difference between the mathematical mind (esprit de géométrie) and the perceptive mind (esprit de finesse): the reason that mathematicians are not perceptive is that they do not see what is before them, and that accustomed to the exact and plain principles of mathematics, and not reasoning till they have well inspected and arranged their principles, they are lost in matters of perception where the principles do not allow for such arrangement. . . . These principles are so fine and so numerous that a very delicate and very clear sense is needed to perceive them, and to judge rightly and justly when they are perceived, without for the most part being able to demonstrate them in order as in mathematics; because the principles are not known to us in the same way, and because it would be an endless matter to undertake it. We must see the matter at once, at one glance, and not by a process of reasoning, at least to a certain degree. . . . Mathematicians wish to treat matters of perception mathematically, and make themselves ridiculous . . . the mind . . . does it tacitly, naturally, and without technical rules.

PASCAL, *Pensées*

Translation of a paper entitled “Om matematik og psykologi – Eller noter om matematik, intuition og virkeligheden (bl.a. hundestjerner)” contributed to a *Festschrift* for Iven Reventlow, June 6, 1986: *Delhed og helhed – Teoretiske og metodiske studier over komplicerede psykobiologiske fænomener*, Copenhagen, 1986, pp. 25-38.

In this quotation, Pascal (1660; 1961, pp. 3-4) sets forth an opposition between mathematical knowledge and more intuitive knowledge. He was himself a proof of the possibility of having these two forms of knowledge living in coexistence within the same person. However, he may still be right in considering mathematical knowledge rough and primitive in comparison to intuitive knowledge.

The Pascal-quotation is used as a motto in Hubert Dreyfus' book, *What computers can't do* (1979), where it is demonstrated that important aspects of existence cannot be understood from such particularly 'rough' forms of applied mathematics, that is, the finite combinatorics that constitute the basis of digital computers, and that the project of making these machines display 'artificial intelligence' is stillborn.

Perhaps one may argue, as some mathematicians and logicians do, that all mathematics in a certain sense possess the same 'roughness', tied as it is by being defined by a finite alphabet. (For a discussion of this, see for example Arbib, 1964, and Crossly *et al.*, 1972.)

However, for many psychologists it will not be the primitive or rough aspect of mathematics that to them brings about a cleft between mathematics and intuition, but rather the inaccessibility and complexity of mathematics compared to the often simpler and immediately given reality. They would also rather say that mathematics with its possibilities of unlimited fine measurement represents a quite unrealistic, irrelevant and excessive accuracy compared to a more 'rough' and qualitative knowledge of reality.

This may look like a paradox. In order to resolve it, we may consider other cases, where there is no cleft between mathematics and intuition.

If we are about to put a football ground under grass, and know the length and breadth of the field, as well as how many kilos of grass seed are going per area unit, then mathematics tells us, without much problem, how many kilos of seed shall be needed. This was perhaps more than we had believed, spontaneously, and although we may accept to be instructed this way, perhaps we cannot help feeling that neither has mathematics done violence to us, nor have our immediate conceptions proved mathematics non-applicable.

And why not? Of course, because the mathematical operations: the measurements of length and breadth, the weighing of the grass seed, and the necessary calculations, are all meaningful and trustworthy depictions of phenomena in the surrounding world.

The application of mathematics is anchored in our practical reality.

Thus the cleft does not subsist between mathematics as such and reality. On the other hand, as we shall see, there is a cleavage between reality and the attempts at a mathematical description of this reality, where the mathematical operations are not themselves practically and conceptually anchored in the same reality as the one to be described.

In the example of ‘computer-mathematics’ and reality, the problem is in fact not the ‘finiteness’ or ‘incompleteness’ of mathematics, or other insufficiencies, but, on the contrary, that the mathematics or combinatorics on which the function of the computer is based, is not anchored in anything else than the computer’s units of reading and writing. Here the cleft consists of the chasm between reality, on the one hand, and the computer keyboard on the other, and not between mathematics proper and reality. Mathematics does not just depict reality if the keyboard does not do it. The computer cannot by itself display human intelligence, since it simply cannot by itself establish contact to the reality in which the human being exercises his intelligence. It lacks the concepts, body, and practice of a human being. (See also Mammen, 1985.)

However, if a user of a computer has *himself* anchored mathematics in reality, then he can use the computer as *a tool* for his calculations to unfold ‘computer-sustained intelligence’.

In the other example concerning ‘excessive’ measurement etc., the problem is, of course, also that the very *operations* that lead to an intelligence quotient with two decimals, or which pile up and count all ‘yes’-respondents to a question in a questionnaire, do not without further ado represent something real in the world (cf. Hem, 1980, Vol. I, Ch. III).

So there is no cleavage between mathematics as such and reality, nor between mathematics and other forms of knowledge, say, intuition or perception, although obviously there is no identity either.

(Regarding this, see for example, the mathematical-historical discussion in Dantzig, 1964, and Klix, 1980, p. 250-56.)

But there is a cleft between descriptions, which obtain their concepts, their foundation, from the described reality itself, and then such descriptions that get them from somewhere else. In fact, the best securing of mathematical knowledge is that it is in agreement with intuition, in so far as intuition itself is anchored in reality. (There may, of course, be exceptions to this.)

Georg Rasch expressed something similar, when he sometime in the beginning of the 1960s taught Iven Reventlow and me the difficult art of statistics: *'What is wrong about the general use of mathematics and statistics is that it is premature.'* And by this he meant that all too often, *inter alia* in psychology, mathematical formalisms were employed and mathematical operations carried out, *before* one had examined more closely whether they correspond to the real structures – that would for instance say, whether such formulations and operations corresponded to the researcher's practical and conceptual understanding of the phenomena under investigation.

During the years 1962 to 1966 I was, as a student of psychology, research assistant to Iven Reventlow and helped with the registration of observations on sticklebacks and, employing GIER-computers, carried out model-testing and estimation of parameters regarding the behaviour of sticklebacks (Reventlow & Mammen, 1964a). It was both fun and instructive. But best of all, I daresay, were our long discussions about ethology, psychology, mathematics, etc., and among them many discussions with Rasch as a participant. The latter discussions took place sometimes in town at the Institute of Statistics, but usually out of town, at Rasch's in Holte, and they were always very animated and wide-ranging, often with overwhelming use of biographical and anecdotal material.

Many of the points from these discussions has Iven given a thorough and clear treatment in his dissertation (Reventlow, 1970), that starts from the stickleback experiments but also to a high degree deals with the possibilities and problems in connection with the use of mathematics in animal and human psychology.

I shall here point to one of the many discussions between Iven, Rasch and me which is mentioned shortly in Iven's dissertation (*op. cit.*, p. 137), where he writes:

'It has been mentioned a couple of times, that one may recognize the animals by their behaviour. Now it is probably not possible to get an immediate impression of the different parameters. However, there is something that seems to indicate, that one may rewrite the formula in such a way, that the mean value of the durations may obtain a relatively simple relation to matters relating to ω and A (or λ and α). This reformulation has, however, not yet been worked out. The reason why the problem is mentioned here is just in order to draw attention to the interesting question inherent in finding out which rewritings of the formula an observer is using in his immediate assessment of behaviour.'

This detached passage requires a bit of explanation:

What Iven observed was *inter alia* male sticklebacks that were rutting and living (most often two together) in an aquarium, where each of them had established a territory and built a nest. The male stickleback alternated all the time between being at its nest and away from it, for example for marking and defending its territory. One of the things that were registered was the length of all the periods, where the fish was at its nest, respectively away from it, during an observation period of 30 minutes. It was always Iven himself who did the observations, while the assistants took down notes after Iven's dictation and looked after the tape-recorder.

Iven had really come to know his fish very well; and when he observed them, he did not see anything else in the room. But, indeed, this the fish did, so therefore everybody participating had to sit quite still. The final proof of Iven's powers of observation was delivered one day, when one of the fish apparently did something unexpected and Iven, without moving his eyes from the aquarium, said to one of the assistants (it was not me and not either the Editor of the present monograph): 'Paul, stop picking your nose!' (The assistant's real name is retained.) Thus caught red handed and immortalized on the tape-recorder, the assistant kept away for a week and had to be persuaded to come back.

The duration of the periods, which the fish spent at and away from their nests, did not present a fixed pattern but were distributed according to a more random pattern. This is, of course, not an uncommon situation in psychology, and nothing had been easier than to calculate the average and dispersion of the obtained time-measurements with a view to a comparison of 'central tendencies' of the durations in different fish or in the same fish under different circumstances.

But this would precisely have been 'premature' according to Rasch's point of view. For such a method would implicitly presuppose a normal-distribution structure for the observations; so this had therefore first of all to be examined, and also if there were theoretical reasons to assume a structure which would imply that the observed distributions could meet the normal-distribution assumption. Neither of them turned out to be the case.

On the contrary, the simplest theoretical assumption would be that, when for instance, the fish was at its nest, there would all along be a fixed probability λ (lambda) that it would leave the nest during the next second. This would correspond to a general 'waiting-time distribution', where the probability that the fish would stay more than T seconds at the nest - that is, the observed time t was greater than or equal to T - would be

$$(1a) \quad P\{t \geq T\} = e^{-\lambda T}, \quad (\text{Reventlow, 1970, p. 59})$$

with the mean value of t being $1/\lambda$.

A graphic analysis of the time-measurements suggested, however, that the model had to be provided with a parameter α (alpha) in addition to λ , so that it obtained the following form:

$$(2a) \quad P\{t \geq T\} = e^{-\lambda T^\alpha}. \quad (\textit{op.cit.}, \text{p. 66})$$

Now it was no more a simple waiting-time distribution, and the probability that the fish would leave its nest during the next second was no longer constant. Only in the very first second this probabil-

ity equalled λ (with some ingenuity). Later it descended, or increased, according to whether λ was smaller or greater than 1.

The new model described the data better than the old one, but this had its price: *Firstly*, it was no longer easy to explain what significance the fact could have theoretically that the observed times followed such a model. *Secondly*, it was very difficult to explain what α and λ stood for. They were difficult to *interpret*. Furthermore, they were very difficult to put in relation to the immediate observation of the fishes' change in being at and away from their nests. And finally, the parameters, especially α , did not show any systematic dependence on the factors that were under study in the experiments.

With regard to interpretation, α could barely be explained as a kind of 'acceleration' of the fishes' inclination for changing activity. Moreover, it was a 'pure number', therefore independent of physical units of measurement. In return it did not manifest any systematics, at all.

As to the other parameter, it was only possible at best to interpret λ as a probability in the very first second of an activity. Then λ had the physical dimension $\text{time}^{-\alpha}$, that is, it had a variable dimension!

The latter problem was, however, solved independently - in fact, for other reasons - when α 's 'accidental character' as an individual parameter was changed into a common, empirically determined parameter $\mathbf{A} = 1.513$ valid for the whole population of fish, and the model therefore took the following form:

$$(3a) \quad P \{t \geq T\} = e^{-\omega T^{\mathbf{A}}}, \quad (\textit{op.cit.}, \textit{p. 69})$$

where $\mathbf{A} = 1.513$.

The successor to λ , that is ω (omega), now had a fixed dimension, namely the unit $\text{second}^{-1.513}$, but had for this reason not become easier to interpret. The same difficulty of interpretation applied to \mathbf{A} , which was now a population parameter instead of an individual parameter like α . And its relation to the immediate observables in the individual fish was radically broken. Consequently the same applied to a certain extent to ω , which was somehow at variance with

the attitude to individual and population parameters generally cherished by Rasch (see for example Rasch, 1960).

An advantage with ω was, that it apparently showed a certain systematic dependence on the factors under examination in the experiments, but consequently a dependence which was only very indirectly in proportion to the observations, and which, because of its awkwardness of interpretation, was difficult to relate to psychological and ethological theory.

But as Iven rightly states (Reventlow, 1970, p. 136): *The psychological interpretation of mathematical expressions depends on which special mathematical expression one chooses to expound.*

And now we have come back to the first quotation.

For it is, indeed, possible to rewrite the formulae in such a way that they become easier to interpret.

The *first* version of the model, for example, may take the following three, quite different forms:

$$(1b) \quad P\{t \geq T\} = e^{-\lambda T} = e^{-T/\tau} = 2^{-T/\vartheta},$$

where $\tau = 1/\lambda$ and $\vartheta = \ln 2/\lambda$.

(It is, of course, possible to choose all sorts of other 'base-numbers' than e or 2 . However, this topic is left out here.)

Both τ (tau) and ϑ (theta) are measured in the dimension time, that is the unit seconds. τ is the mean value of the distribution; ϑ is its *median* and therefore the value where the probability stating that the time is longer, or shorter, are both $1/2$. If a large number of fish, that follow the same distribution, and therefore with the same ϑ , start simultaneously by being at their nests, then precisely half of them will still be at their nests after ϑ seconds. Thus ϑ is the 'half-life period' of the distribution, cf. the corresponding concept in the decay of radioactive isotopes.

If we have a long row of duration-measurements of the same fish at its nest, then half of the durations will be shorter than ϑ and the other half longer than (or equal to) ϑ .

It now turns out, that the *second* version of the model may also be rewritten in this way:

$$(2b) \quad P\{t \geq T\} = e^{-\lambda T^\alpha} = e^{-(T/\tau)^\alpha} = 2^{-(T/\vartheta)^\alpha},$$

where $\tau = \lambda^{-1/\alpha}$ and $\vartheta = (\lambda/\ln 2)^{-1/\alpha} = (\ln 2/\lambda)^{1/\alpha}$.

Now τ is no longer the mean of the distribution, so this one we shall leave aside. However, $P\{t \geq \vartheta\} = 1/2$, and therefore ϑ is still the *median* of the distribution!

Further, this reformulation of the formula permits also a certain interpretation of α , at any rate a rather simple coupling to the observed distribution. If, namely, ϑ' is that value for which $P\{t \geq \vartheta'\} = 1/4$, i.e. the theoretical value for the distribution's upper quartile, then $\log(\vartheta'/\vartheta) = \log 2/\alpha$. Or, in other words, if $\alpha = 1$, then $\vartheta' = 2\vartheta$, if $\alpha > 1$ then $\vartheta' < 2\vartheta$, and if $\alpha < 1$, then $\vartheta' > 2\vartheta$. If $\alpha = 1$, then the distribution is 'non-accelerated' as it were, which means that after respective 1, 2, 3, etc. times the 'half-time period' ϑ , there will be respectively $1/2, 1/4, 1/8, \dots$ 'left' of the distribution. If $\alpha > 1$, then the 'reduction' goes faster, whereas with $\alpha < 1$ the 'reduction' will be slower.

When, finally, looking at the *third* version of the model (leaving τ out), we get

$$(3b) \quad P\{t \geq T\} = e^{-\omega T^A} = 2^{-(t/\vartheta)^A},$$

where $\vartheta = (\ln 2/\omega)^{1/A}$, and $A = 1.513$.

Again ϑ is the *median* of the distribution.

Therefore ϑ is a parameter, that has the same firm coupling to the observed distribution, irrespective of which of the three models one chooses!

Let us then resume the characteristics of the parameter ϑ :

(1) As opposed to λ and ω , ϑ has the physical dimension *time*, and is thus measured with the same units as the observed times.

(2) ϑ can be interpreted as the time, where there is 50% probability of the fish having stopped its activity. Regarding fish with not too different α , or given a constant $\alpha = A$, then a small ϑ means a great tendency for interrupting the activity, and inversely a large ϑ means a small tendency to interrupt the activity.

A direct coupling to a simple biological mechanism is no easy matter in the two-parameter model as it is in the one-parameter model ($\alpha = 1$), where the half-life period ϑ corresponds to a constant tendency or probability per second $\lambda = \ln 2 / \vartheta$ for interrupting the activity.

Therefore ϑ does not have a very simple psychological or biological interpretation in case of variable α , but is nevertheless as a behavioural measure reasonably understandable and communicable, and for large differences in ϑ and small differences in α also a reasonably good standard of comparison for different distributions.

Assuming a constant $\alpha = A$, then ϑ may even be expounded as the fish's internal (though always conditioned by the whole situation) 'unit of time-measurement', or 'biological clock', as all distributions become identical if t is measured in ' ϑ -units'.

In all cases ϑ is much less 'cryptic' than λ and ω .

(3) Supposedly one of the properties of a distribution of observed times, that can be perceived directly by an observer, independent of any calculations, will be just the 'level' of the distribution, understood as its average time or its quartiles. As median in the distribution ϑ will be such a property, or at any rate, it may correlate rather strongly with it.

It is quite conceivable therefore that there is a good connection between ϑ and a more intuitive way of observation, which, of course, may also be 'educated' by practice.

(4) ϑ has the advantage, in comparison to λ and ω , that it corresponds to a well-established and communicable parameter for an observed distribution - namely, the median.

(5) With access to a computer, all parameters α , λ , ω , and ϑ may easily be estimated on the basis of a typed-in distribution. But ϑ

can, as a matter of fact, be estimated without a single calculation, since one only has to write down the observed times and then count up to the one(s) in the middle starting from the shortest or the longest. (In paying attention to the upper quartile, one may even with a pocket calculator obtain a quick estimate of α , in remembering that $\log(\vartheta'/\vartheta) = \log 2/\alpha$.)

Such estimations 'on location' permit a more efficient relation between 'experimentation time' and 'calculation time'.

Moreover, the calculations printed in the Appendix to the dissertation (Reventlow, 1970, pp. 206f.) show a very good accordance between $\vartheta = (\ln 2/\lambda)^{1/\alpha}$ and the empirical medians of the distributions. (ϑ and the empirical medians vary from about 4 seconds to about 180 seconds.)

(6) As a theoretical median of the distribution ϑ may be estimated by the empirical median of the distribution independent of any assumption as to whether α is constant or equal to \mathbf{A} , or not. A comparable independence does not hold for estimations of λ and ω .

(7) It has not been directly examined, whether the estimations of ϑ varies systematically dependent of the factors under study in the experiments. However, it looks as if the estimates of ω vary systematically. Furthermore, since the theoretical values, viz. the parameters ϑ and ω , are firmly connected via the formula $\vartheta = (\ln 2/\omega)^{1/\mathbf{A}}$, then it may be assumed that the estimation of ϑ also varies systematically dependent of the factors investigated in the experiments.

It is probably point (7), which Iven had in mind when he, in the above quotation, said, that the reformulation had not yet been worked out. (Incidentally, I am convinced that he meant 'the median' when he, in the quotation, wrote 'the mean value'.)

The other points, however, were both worked out and discussed with Rasch with a view to a reformulation of the model. But he stuck to his opinions, and there the matter rested.

I attempted some more technical arguments concerning the estimation methods and their dependence of dimensions and invariants in estimates and parameters, but it was waste of energy.

To be sure, we received later, also on that point, support from Benny Karpatschof in his opposition to Iven's dissertation, and additionally in Benny's paper, 'Scale-invariant Probability Models' (Karpatschof, 1971), which contains a profound treatment of the problems discussed here.

So in defiance of all the right principles about respecting the structure of the data material etc., cherished by Rasch, he had by all appearances lead us away from the reality that was to be investigated. But why?

One of the reasons could be, that the expressions with α and λ were mathematically convenient and facilitated the theoretical development of estimations of the parameters on the basis of moments (*in casu* mean value and dispersion) in the distribution of $\log t$. The same applies to ω .

This could, however, not be a principal argument, since the estimates (including their variances and co-variance) of ϑ and α could easily be derived from estimates of λ and α . And similarly for ϑ and ω .

Perhaps the discord in reality turned around a central concept regarding interpretation of the model, namely *the intensity function*, that is, the probability of the fish leaving its nest during the next second, provided that it is still at the nest after T seconds. The intensity function is thus an expression for the very *tendency*, which the fish has for leaving its nest at any moment, whether it does it or not. (Similarly for the fish away from its nest.)

In other words, the intensity function permits an interpretation of an observed distribution in terms of an underlying tendency, 'tension' or perhaps 'motivation' as a function of time.

Mathematically the intensity function may be defined by

$$i(T) = -d \ln P\{t \geq T\}/dT,$$

and we then obtain for the three different versions of the model, respectively:

$$(1c) \quad i(T) = \lambda \quad = \ln 2/\vartheta,$$

$$(2c) \quad i(T) = \lambda \cdot \alpha \cdot T^{\alpha-1} \quad = \ln 2/\vartheta \cdot \alpha(T/\vartheta)^{\alpha-1},$$

$$(3c) \quad i(T) = \omega \cdot A \cdot T^{A-1} \quad = \ln 2/\vartheta \cdot A \cdot (T/\vartheta)^{A-1}.$$

Equation (1c) describes the simple ‘waiting-time distribution’ with a constant intensity λ (see Rasch, 1960, p. 39).

Equation (2c) describes the two-parameter model, where the intensity is an increasing function of T for $\alpha > 1$ and a decreasing function for $\alpha < 1$, and therefore, as said earlier, a positively, respectively negatively ‘accelerated’ distribution. It will be seen that for $\alpha = 1$, the intensity is constant, equal to λ or $\ln 2/\vartheta$.

Equation (3c) describes the model with a fixed $\alpha = A = 1.513$, viz. a distribution with an increasing intensity, or a steadfast ‘positive acceleration’.

The expressions to the left of the second equals sign in the three equations define the intensity in terms of the parameters λ or ω and α or A .

The expressions to the right define the intensity in terms of the parameters ϑ and α or A .

The left-hand and right-hand expressions are obviously quantitatively equivalent, but Rasch preferred the left-hand ones, and the rest of us the right-hand ones? But why?

I believe that Rasch preferred the left-hand sides because they, considered as *pure mathematical expressions* were simpler and more elegant than the right-hand sides, and because the left-hand sides in (2c) and (3c), considered as mathematical expressions, were clearly in family with, or a ‘generalization of’, the constant λ in ‘the waiting-time distribution’ (1c).

The reason why Iven and I preferred the right-hand sides was – in continuation of all previously given reasons – that the right-hand sides were at least meaningful as *physical expressions*, as it were, which did not apply to the left-hand sides. A physicist would make the sign of the cross in front of the dimensional ‘mess’ that characterize the left-hand sides in (2c) and (3c), and alone for that reason ready

to say in advance, that λ and ω here were not interpretable in relation to physical reality.

The intensity function $\mathbf{i}(\mathbf{T})$ has always the dimension time^{-1} , just as λ in (1c), which is not difficult to interpret. But in (2c) and (3c) λ and ω now suddenly, as said before, have got the dimensions of respectively $\text{time}^{-\alpha}$ and $\text{time}^{-1.513}$, and with α as a ‘pure number’.

The right-hand sides, on the contrary, are in any case, *simple with regard to dimension*, since α is still a ‘pure number’ and ϑ has the dimension time in all three versions of the model.¹

But, besides, it does not look as if the intensity function is the only basis for the interpretation of the model and the parameters.

The main reason for mentioning the intensity function here is that the disagreement about its formal definition illustrates very well a difference between a ‘pure mathematical-statistical’ attitude and a more ‘physical’ attitude to the formulae, where the latter through its demand of *dimensional order and lucidity* is a reminder that any truthful description – also a mathematical depiction of reality – is always both *quantitative* and *qualitative*, and that the description will become remote from reality, if the qualitative side is ignored.

Time has now come for summing up the characteristics of the ϑ -model, which at the same time aims at a *generalisation* and thereby indirectly put forward a number of *ideal requirements* to a parameter (cp. the 7 points, above):

1. ϑ is a *quantity* in the same *quality* (namely time) as the observations.
2. ϑ can be *interpreted* in relation to the *concepts* in which the investigated, dynamic system may be understood (either as tendencies for change of activity or as a ‘biological clock’) and may therefore be used for *comparison* between dynamic units (individuals under various conditions).

1. No postulate is here implied that physical *expressions* may not have variable dimension, or that a parameter, which in itself is without dimension (like α), may not be a dimension variable. But it is a premise, if a physical term is going to specify its (perhaps variable) dimension unequivocally, that the very basic, inherent *parameters* do have a fixed dimension.

3. ϑ is closely coupled with or *corresponds* to the *immediate observations*, but gives a more precise and stable picture than these.
4. ϑ describes a relatively *simple* and *communicable* property of the set of observations (namely, the median of the distribution).
5. ϑ can be estimated immediately without advanced facilities. That is to say, an *estimate* may be made on the spot (followed up by calculations, if necessary).
6. ϑ can both be defined and estimated for a *single individual* independent of suppositions on population parameters (*i.e.* independent of whether $\alpha = \mathbf{A}$).
7. ϑ may show a *systematic dependence* upon other factors in the dynamic system under examination.

In the case considered, it looks as if there is a remarkable parallel in the way the requirements are met. Apparently the requirements do not compete, but 'help' each other.

This is hardly an accident (apart from the fact, that we have been particularly fortunate in point 5), but it is connected with the situation that all the requirements have to do with representations of the same dynamic property of the examined system.

Of course, one may come in other situations, where the fulfillment of some requirements, for example point 7, clashes with some of the remaining ones, for which reason they must be abandoned. From physics there are also known examples, where not all requirements are fulfilled.

But especially these examples have clearly illustrated that in such a situation it is necessary to have a fundamental discussion about the relation between the *theoretical* concepts, the *practical* operations, and the *intuitive* understanding. Thus mathematical or quantitative description evokes a conceptual or qualitative discussion and clarification.

And so it has to be, even though it may be arduous and require patience.

As far as I know, Iven Reventlow's dissertation is unique in Danish psychology for its thorough discussion of these problems. At the same time, it also illustrates the great difficulties such a work has to face, as it is partly an interdisciplinary pioneer work (human psychology, ethology, and mathematics), partly both empirical and theoretical, and, not the least, presupposes collaboration between researchers where no one wishes to follow the line of least resistance.

By calling attention to this work, I hope to have illustrated that a consistent continuation of the principles, which lay at the root of this collaboration, does not lead to unrealistic mathematical 'formalizing', but on the contrary points forward to a true-to-nature picturing of the phenomena, which at the same time is practically, intuitively, communicatively, and theoretically meaningful.



From the public defence of his dissertation, April 14th 1970, Reventlow (to the left) is here seen with the opponent *non-officio*, Dr. Georg Rasch, in dispute over the interpretation of a graphic representation. On the first row in the auditorium are seen from behind the psychology professors Edgar Tranekjær Rasmussen (to the left) and Franz From. Reventlow later related that, to his great annoyance, he was unable to penetrate the opponent's torrent of speech with his rejoinder - prepared for countering such a criticism - namely, that the mathematics employed and the model had been adopted after meticulous considerations in concert with his statistical consultant, Professor Georg Rasch. (Photo, Jens Mammen.)

Postscript by Jens Mammen (2018): A Science Thriller

A statistical model must, as any applied mathematical model, map the empirical structure in the set of data as accurate as possible. But this is not enough. The model and its parameters must also be meaningful. It must be possible to interpret the parameters in relation to the logic, the dimensions and the dynamics in the objective reality studied and in our experimental or observational interactions with this reality, which produce the data. The model should sharpen and refine our intuitive understanding of the phenomena studied, and perhaps correct it, but not cut the bridge to intuition completely.

JM

After 32 years some words have to be added to my above contribution to Iven Reventlow's *Festschrift* in 1986 (hereafter: 'my *Commentary*').

When re-reading my *Commentary* it is evident that the problems I address, although appearing rather severe, are being understated. As a research assistant on Iven Reventlow's investigations on sticklebacks leading to his doctoral dissertation in 1970 I had been very close to Iven and knew his troubles and his disappointments. I knew his large-scale empirical plans and his far-reaching hypotheses concerning the motivational organization of behavior of the animals studied, and that problems with the suggested mathematical model took too much time and energy from the empirical project.

The *Festschrift* was, however, not the place to reopen the wound although its causes could not be silenced. What Iven Reventlow despite these problems had accomplished, was still impressive. The

Postscript to the above *Commentary* written in 2018 for the present publication.

title of the *Festschrift* was “*Part & Whole. Theoretical and methodological studies on complicated psychobiological phenomena*”. I think Iven was happy with it. But I guess he would have been even happier if the title had included “*empirical studies*”.

The source to Iven’s troubles should first of all be found in the co-operation with his statistical consultant.

Iven Reventlow was a psychologist and an ethologist, but he was not a professional statistician, and had to rely on his statistical consultant, professor Georg Rasch (1901-1980, see Wøhlk Olsen, 2003; Juul, 2007). It was Rasch who developed the models for describing the patterns in the empirically observed durations of time between the sticklebacks qualitative changes of behavior, *e.g.* from the fish being at its nest to leaving its nest.

The first approximation was a simple model for these durations or ‘waiting times’ with one parameter λ (lambda) as described in equation (1a) in my *Commentary*. But soon Rasch had to modify it to a model with two parameters, λ and α (alpha), as described in equation (2a), where λ and α were parameters specific for both the individual fish and for the individual type of activity.

This model did, however, not allow independent estimation of the two parameters from the observed durations, and it was therefore, after much discussion and calculation (Reventlow, 1970, pp. 66-70), decided to replace the parameter α , specific for the individual fish and the individual situation, with a parameter $\mathbf{A} = 1.513$ common to all fish and all types of activity and only let the other parameter be specific for the individual fish and the individual situation as described in equation (3a). Not to mix up the two models the specific (for fish and activities) parameter λ was now replaced with a specific parameter ω (omega).

The main reason given was that it could not be empirically refuted that the parameter \mathbf{A} was common to all the fish and types of activity.¹ But a weighty reason was also, as mentioned, that the two-parameter model (2a) did not allow independent estimations of both α and λ and that the specific parameter λ (hereafter ω) could not be sacrificed, as it obviously showed big individual and situation-specific variability, and further, because ω should serve as de-

pendent variable in experiments with the fish in different settings and conditions serving as basis for independent variables.

Not all problems concerned, however, the replacement of λ with ω , or in other words, the replacement of the λ and α model (2a), with the ω and A model (3a). There remained some serious problems of interpretation common to the two versions of the model, because both the parameters λ and ω were difficult to interpret in relation to the observations, as already discussed in my *Commentary* (1986).

To understand the remaining problems with the two models, and especially how they were discussed, we shall once more return to the quotation from Iven's dissertation (Reventlow, 1970, p. 137) cited in my *Commentary*.

'It has been mentioned a couple of times, that one may recognize the animals by their behaviour. Now it is probably not possible to get an immediate impression of the different parameters. However, there is something that seems to indicate, that one may rewrite the formula in such a way, that the mean valueⁱⁱ of the durations may obtain a relatively simple relation to matters relating to ω and A (or λ and α). This reformulation has, however, not yet been worked out. The reason why the problem is mentioned here is just in order to draw attention to the interesting question inherent in finding out which rewritings of the formula an observer is using in his immediate assessment of behaviour.'

When Iven here writes "This reformulation has, however, not been worked out", what is told between the lines is that Rasch, despite several requests, ignored or refused the proposed reformulations, and that Iven did not want to challenge his statistical consultant in the dissertation. Iven and I had persistently, verbally and in the form of notes, asked Rasch to replace his model with the one proposed in my *Commentary*.

I will here bring some quotes from a letter sent by Iven to Rasch July 6, 1964, which we both formally signed (Reventlow & Mammen, 1964b). There is in the beginning reference to an earlier note (My translation from the Danish):

'Dear Georg! As I wrote to you, Jens and I have been playing with our models. [...] I would try to look at some transformations of the formulas in the model hoping to find some better psychological interpretations [...] and because of the difficulties with lambda [...] I worried if I [...] had accepted alpha and lambda as important concepts without really thinking out if they had psychological relevance. Therefore I had Jens to help me with transformation of the formulas. We came to the following which [...] I think will be more meaningful for most psychologists than alpha and lambda. Which of the parameters you finally choose to work with can presumably only be decided by testing them in many different psychological situations. [...] With α and τ the model looks this way

$$(1.1) \quad P_+\{t\} = e^{-(t/\tau)^\alpha}$$

This could also be written

$$(1.2) \quad P_+\{t\} = 2^{-(t/\tau_1)^\alpha}, \quad \text{where}$$

$$(1.3) \quad \tau_1 = (\ln 2)^{1/\alpha} \cdot \tau \quad \text{[...]}$$

This last version of the model now implies, that

$$(1.4) \quad P_+\{\tau_1\} = 0.5,$$

or, that τ_1 is the median of the distribution.

[...]'

$P_+\{\mathbf{t}\}$ here means the probability that the observed duration is bigger than \mathbf{t} , in other words the reverse cumulated distribution $P_+\{\mathbf{t}\} = 1 - P_-\{\mathbf{t}\}$. The parameter τ (tau) has the dimension time as also the proportional parameter τ_1 , which in my *Commentary* is called ϑ (theta).

The rest of the letter to Rasch describes some of the advantages of our proposed model mentioned in my *Commentary* in the *Festschrift*, e.g. that τ_1 (in the *Commentary* ϑ) is the median in the distribution independent of α , and also some technical questions concerning esti-

mation, especially the possibility of independent estimations of τ (or ϑ) and α . This possibility would further have prevented the later severe problems with the common parameter \mathbf{A} , forced on the data. Behind the reference in our letter to “*the difficulties with lambda*” were estimation problems, but first of all that a parameter as λ with a continuously varying dimension, or as ω with dimension ‘time in the potency -1.513 ’, in this investigation $\text{sec}^{-1.513}$, are monstersⁱⁱⁱ, impossible to interpret outside their function in the formulas, while the τ or ϑ variables, with the dimension ‘time’, can be related to *e.g.* ‘biological clocks’. Further, there was Iven’s ambitions, partly inspired by Rasch, to ‘break up’ the parameter for a certain fish and a certain condition or environment in, respectively, a ‘prority’ parameter and an ‘exposition’ parameter (‘components’ or ‘sub-parameters’), that could as well have been performed on the τ parameters as on the ω parameters. Nothing in the theoretical or methodological frame had to be changed, but the interpretations now had been *transparent* because they could be related simply to ‘biological-clock’ functions and to the observations, phenomenologically and quantitatively^{iv}.

The main points are that the parameters in our alternative model are easy to interpret psychologically and to explain to colleagues, and especially the parameter τ_1 (*i.e.* ϑ) is almost directly observable and easy to estimate from the observations without complicated calculations.

From a practical experimental perspective the last quality of our alternative model means that one almost immediately after an experiment can have a rather good estimation of the parameters, and that more accurate calculations and estimations of confidence can wait until the final report. In Iven’s experiments this was a *sine qua non*. Often the next series of experiments depended on the outcome of the present ones, as new hypothesis about motivational levels and hierarchical organization of behavior were dependent on confirmation or refusal of former hypotheses. And the sticklebacks were short-living and their motivational programs also rather ephemeral. So you had to decide while the fish were alive and in the same state of rut.

But first of all Iven's whole approach and 'style' was the highly trained and intuitively guided observations of the species studied. He really knew the sticklebacks, and although also interested in theory and methodology, observations and experiments with some immediate 'transparency' to guide creative thinking was what he loved and mastered.

In my view Rasch's model instead became a wall between the observer and the phenomena. The process of estimating parameters was indirect and complicated. If I had not developed a computer-program for the calculations and primitive graphs, it would have been even worse. At that time, around 1964, there were only three or four computers (GIER-machines programmable in Algol-language) available in Copenhagen, and I had for a long time only access to one or two of them where I had to book machine-time days before in competition with other researchers to conquer one half hour if lucky. If Iven had not, through his acquaintance with professor Bengt Strömngren, managed that I could use the GIER-machine in the University's Astronomical Observatory next to Botanical Garden of Copenhagen at night-time, all alone, with screwdriver and repair kit, the calculations would have been further delayed. This machine was not part of the booking system, and nobody used the observatory at night-time. After the sky over Copenhagen became illuminated at night the observatory from 1861 had no nocturnal obligations anymore.

To make a long story short, Rasch would not listen and was, despite his role as a consultant, insensitive to Iven's demands, and Iven's empirical plans were suffocated, more or less. Instead of giving up Iven heroically and successfully changed his project to mainly theoretical and methodological and with far-reaching analyses and conclusions. But it was plan B.

When Iven April 14, 1970, publicly defended his dissertation for the doctor's degree Benny Karpatschof, who is both a psychologist and a statistician, in his opposition raised the above issue and took Iven's and my side against Rasch's with explicit reference to our written notes on the question. In the preface to a later publication (Karpatschof, 1971, pp. iii-iv; my translation from the Danish) Karpatschof referred to:

“the result verbally published in my opposition *ex officio* at Reventlow’s public defense, namely that the only sensible models for waiting times are scale-parameter models [...] anticipated in a mimeographed note by mag.art. Jens Mammen to Reventlow.”

As I heard it this was not a matter of opinions but rather an ascertainment that Rasch’s model, with the parameters λ or ω , used by Iven in his dissertation was flawed. And this conclusion was hereafter not concealed in the scientific milieu around Iven Reventlow.⁹

This is what I knew when in 1986, 16 years after Iven’s dissertation, in my *Commentary*, I wrote my retrospect for the *Festschrift*.

But when finally I received the volume I got a surprise. Three other contributions to the *Festschrift* (Damgaard Petersen, 1986a; 1986b; Voetmann Christiansen, 1986) also wrote about the two-parameter-model used by Iven in his dissertation 1970, but they did not mention Georg Rasch and did not refer to Rasch’s formulas used by Iven. And even more strange, both authors referred to the model as the Weibull-distribution. I had never heard of that, not being a statistician, and I am sure that neither Iven nor Rasch ever mentioned the name Weibull or the Weibull-distribution in my presence. In that case I would have asked what that was. So I am rather convinced that Iven also never heard of it. In any case he never mentioned it in his writings.

I was in 1964 a third year psychology student, but had some scientific background from an earlier study of mathematics and physics, and had developed the rather trivial and obvious proposed model myself by analogy with the formula for radioactive decay, cf. formula (1b) in my *Commentary*.

My surprise was not less when I, in Voetmann Christiansen’s contribution (1986, p. 39), instead of Rasch’s and Iven’s formulas, saw the formula for the reverse cumulative Weibull-distribution, or the Weibull ‘survival function’ $P_0(t)$

$$(1) \quad P_0(t) = e^{-(t/\tau)^\alpha}.$$

This was exactly the model Iven and I had requested in 1964 (and in fact both before and after), but which Rasch had refused, and

even with the Greek letter τ chosen as the ‘time scale parameter’. Iven never referred to it in his publications! But the readers of the *Festschrift* were made believe that Iven used the Weibull-model, and accordingly its parameters α and τ .^{vi}

As mentioned above we also in our letter to Georg Rasch (Reventlow & Mammen, 1964b) proposed the equivalent ‘proportional’ distribution with ‘basis’ 2 instead of e , and parameter τ_1 (in my *Commentary* ϑ), confer the equations (1.2),(1.3), and (1.4) in the above cited letter, for its interpretative virtues as the distribution’s median (or ‘half-life period’ in physics) *independent* of α . This independency further makes τ_1 , or ϑ , very ‘robust’ in relation to the empirical observations.

Some questions immediately arose about both Rasch’s refusal of Weibull’s model and about the strange omissions in the above-mentioned three contributions to the *Festschrift*.

In fact, although everybody knew about Iven’s extensive use of Rasch’s model in his dissertation and some of the authors also were inspired by this model and even had used it, nowhere in the 216 pages *Festschrift* was Rasch’s name even mentioned, except in my contribution and in a short reference to Rasch’s concept of specific objectivity, in (Dollerup & Rosenberg, 1986), but not to the waiting-time model used by Iven.

I left Copenhagen and the circles around Iven Reventlow in 1968, was fully occupied with psychology at Aarhus University, and did not follow what happened except attending Iven’s public defense of his dissertation in 1970. The *Festschrift* in 1986 implied a lot of questions.

1. Did Rasch at all know the Weibull-distribution? I much later found out that it was rather well-known and already in 1951 described in detail by the Swedish statistician Waloddi Weibull (Weibull, 1951), although older. It would be strange if a professor in statistics in a neighboring country did not know of it.

2. If Rasch knew the Weibull-distribution, which he must have, why did he not propose it as a model for Iven’s data? It was already well-described, its advantages in separating a ‘scale’-parameter τ (in the

present interpretation with dimension ‘time’) and a ‘form’-parameter α (dimensionless) was generally acknowledged, and the estimation problems had been well elaborated. It was so to say ‘ready to cook’ and would have saved oceans of time and besides being theoretically and empirically transparent.

3. If Rasch had his reasons not to prefer the Weibull-distribution why did he not even mention it, and why did he not tell Iven and me that what we proposed was in fact the Weibull-distribution, and consequently explained to us why he refused to use it?

4. Why did Voetmann Christiansen and Damgaard Petersen in their contributions to the *Festschrift* claim that Iven used the Weibull-distribution while nowhere mentioning that he had used Rasch’s ‘clumsy’, and in fact inapplicable, version with the unfit parameters λ or ω ? Why did they not tell that Iven himself never mentioned Weibull? And why did they never mention Rasch who in fact was responsible for Iven’s two-parameter model?

5. If Voetmann Christiansen and Damgaard Petersen^{vii}, who cooperated with Iven, knew of the Weibull-distribution while Iven was fighting with Rasch’s unfit model why did they not tell him? Did nobody dare to correct Rasch? And was this possible conflict still embarrassing in 1986, six years after Rasch’s death?

None of the persons referred to are living today (Iven Reventlow died 2003), and perhaps we will never get the full answers, despite the fact that this is no academic splitting hairs, but is about impediment of a promising empirical research project. The virtues of a statistical model is not just to match the empirical pattern in the data as Rasch’s model did, but also to provide parameters which can be interpreted in relation to the object of study which generates the pattern. And this bridge to reality was broken in Rasch’s model, although the same bridge was close to being a mantra in Rasch’s writings on specific objectivity and in his critique of much ‘main stream’ statistics. Further this bridging, or objective mapping of the object studied, is in Rasch’s understanding a *sine qua non* for a model’s practical relevance!

Maybe we can, however, get some help from a thorough and comprehensive ph.d.-dissertation written by Lina Wøhlk Olsen on Georg Rasch and his contributions to statistics (Wøhlk Olsen, 2003).

This dissertation not only offers an overview of Rasch's contributions to statistics but, as the title indicates, also an exposition of his professional life and career, and to some degree, his private life. There is no reference to Rasch's connection with Iven Reventlow or to the kind of models Rasch developed in this context or to Weibull's models.

First of all it is evident, that Rasch was an extremely original and creative scientist, and that he had made most important and even revolutionary contributions to statistical theory and practice. Today he is considered one of the world's greatest modern statisticians with lasting importance for *e.g.* theory of measurement in psychological science. At the same time he is described as very eccentric, both in his behavior and in his nearly monomaniac focusing on his own theories and methods and disregard of others'.

As long as Rasch could dominate the scene he is described as generous and caring, but if meeting resistance he could be "*very rude*" (p. 39) and "*extreme outbursts were not one-off events*" (p. 150).

Rasch was widely feared, and Wøhlk Olsen writes (p. 36), quoting a colleague, that

"Rasch ... was a terror to medical doctors when he appeared at their vivas and criticized their use of statistics. The clever guys used him instead as a consultant. Then all eventualities were covered".

It was evident that it was no pleasant experience to openly disagree with Rasch^{viii}.

Rasch wrote in 1968-69 (with the help of loyal assistants) a comprehensive textbook in statistics to be used at university level (Rasch, Christiansen & Stene, 1968/1969). This seems to be the only place (Vol. 1, pp. 267-274) where Rasch writes about his generalized two-parameter model for waiting times used in the stickle-back experiments, cf. the above equation

$$(2a) \quad P\{t \geq T\} = e^{-\lambda T^\alpha}$$

It is, however, striking that W. Weibull, who in fact is the recognized originator to the model (in this or other versions, cf. note vi), is not mentioned here or anywhere in the book. Even more peculiar is it that Iven Reventlow and his experiments are also not mentioned with one word, and that the only example given is from an investigation of offences and sentencing with no reference to the source.

A review in 1970 of this textbook tells much about both Rasch and his relation to contemporary colleagues. Wøhlk Olsen writes (p. 170):

“The review also drew attention to the fact that Neyman Pearson test theory was not even mentioned, and that the book might as well have been written in the 1930’s, since no new statistical theory except that of Rasch’s was included”.

This perhaps precise, but not very friendly, review was written by Christer Weibull (Weibull, 1970) a relative to the before mentioned Waloddi Weibull. Wøhlk Olsen doesn’t mention any direct communication between Rasch and C. Weibull and makes no reference at all to W. Weibull.

It is unknown what the relations had been between Rasch and W. Weibull. But it might not be so surprising, after all, and after consulting Wøhlk Olsen’s dissertation, if Rasch was not inclined to refer to Weibull or his model, and that nobody else wanted to do it while Rasch had his dominating position. But why the relation between Rasch’s and Weibull’s models and their conflicting use of parameters, although well-known, could still not be mentioned in the *Festschrift*, in 1986, six years after Rasch passed away, is a mystery. If the relation between the two models (or versions) was unknown, there would be no reason to mention Weibull at all in the *Festschrift*, and perhaps this reference to Weibull was an indirect way to communicate Rasch’s defeat and a dissociation from Rasch without even mentioning his name.

Apparently there has from the late 1960's been some personal discrepancy between Rasch and Iven Reventlow and his circle, including some of the contributors to the *Festschrift*, cf. Arne F. Petersen's *Editorial Note*. But that it should cause a total silencing from both sides is unusual in science, and misleading for posterity.

However, the data are still available, the general approach is still valid, and with more suitable mathematical models the conclusions may still be far-reaching. The problems caused by an unlucky cooperation with the statistical consultant does not invalidate the fact that Iven Reventlow did an important pioneering achievement for psychological science.

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Notes

i To replace α with \mathbf{A} was a result of much discussion and calculation (see the treatment of this issue in Reventlow, 1970, pp. 66-70) and mainly motivated by the fact that the model described in equation (2a) did not allow independent estimation of the two parameters λ and α . The decision, finally, to replace all the specific α 's with a common fixed parameter \mathbf{A} for all fish in all situations was first of all an improvised solution and the test presented (*op.cit.*, p. 69; and p. 39 *above*) to reach this 'convenient' solution was in fact irrelevant in relation to the issue in question. The test was a χ^2 -test applied on 106 estimated specific α 's obtained from 14 different situations or "series" (and one supplementary series with 8 α 's not reported in the dissertation), again based on 2255 individual observations (See *op.cit.* appendices 1-5, pp. 206-213). What was tested was whether the 15 different distributions of individual α 's in the 15 different experimental situations or series had the same mean-values. This hypothesis could not be refuted, as the test did not come out with a significant value. In other words: the test said something about the (insignificant) differences *between* the 15 distributions of α 's. It did not say or test anything about the distribution of α 's (for the different fish) *within* any of the 15 distributions and their relation to the distributions' mean-values, which also would be impossible without a theoretically derived variance to compare with the empirical dispersions.

You could perhaps say that what was interesting was the parameters' dependence of the situations, and that apparently only ω showed such dependence. However, the whole philosophy of the investigation and its general purpose was for the individual fish and the individual situation to separate the parameters in an individual component and a situation component, which meant that you could not ignore that the parameters should have validity in relation to the individual fish. The estimation of ω for the individual fish had in fact the value of the common parameter \mathbf{A} (and not its own individual parameter α) as a premise, and this premise was, as demonstrated, not justified by the test mentioned, but forced on the data by

Rasch in an attempt to neutralize the consequences of an unlucky choice of the basic model.

On top of this the test used (*op.cit.* p. 69) is designed to compare distributions with no linkage or coupling. But the distributions were in fact highly coupled as far as all 2255 observations and all 15 series with a total of 106 α 's were only based on seven individual fish. If a test had been used designed for this case the significance may have been much larger. This flaw is, however, without importance as the test already is irrelevant for the issue in question.

ii As it appears from the letter quoted above (Mammen & Reventlow, 1964b) 'mean value' should have been 'median', cf. p. 99 in my 'Commentary' (1986).

iii If *e.g.* time is measured in seconds, and the median in the observed times is $\vartheta = 60$ sec., which is within the range found in the experiments, we would have $\omega = 0.001414 \text{ sec}^{-1.513}$, cf. equation (3b). If, however, the time is measured in minutes we would of course have $\vartheta = 1$ min, but now we will have $\omega = 0.6931 \text{ min}^{-1.513}$, with no transparent relation between the two measures for ω . This reasoning is an example of so-called *dimension analysis* which is used recurrently in both the above *Commentary* (1986) and this *Postscript*. Dimension analysis is about the deep interdependence between the qualitative and quantitative order in nature. There is a recent, very clear and instructive introduction to the method in physics in Jensen & Hecksher (2018), written in Danish but with further references to international literature. It is claimed that the method should be used more both inside physics and, especially, outside physics. Statistical modeling is, in my view, an obvious target for this request. I think it is no accident that the paper is written by researchers from the institute (IMFUFA, Roskilde University, Denmark) where Peder Voetmann Christiansen for years was a driving force. As already mentioned, Voetmann's proposal (1986, p. 39) of an alternative model in the stickleback study is strictly following the demands of dimension analysis.

iv *Possible, but insufficient, arguments for choosing the \mathbf{A} and ω model:* One argument for choosing the \mathbf{A} and ω version of the model could, as mentioned in my above *Commentary*, pp. 101f, be that ω becomes a simple factor in the so-called *intensity function* $\mathbf{i}(\mathbf{T})$, cf. the left-most expression in equation (3c) $\mathbf{i}(\mathbf{T}) = \omega \mathbf{A} \mathbf{T}^{\mathbf{A}-1}$.

The intensity function, with the dimension time^{-1} , describes the probability of the fish ending its activity during the next second, provided it is still active, or in other words: the intensity function is an expression for the fish's *tendency* to end its activity at the moment \mathbf{T} . This means that ω could be interpreted as the specific *level* of this tendency, where the *form* of its development in time is common for all observations equaling $\mathbf{A} \mathbf{T}^{\mathbf{A}-1}$.

Further, one possible understanding of the dynamics behind the fish's behavior could thus interpret ω as an indicator of *motivational level*, of course leaving out the problems with estimation of a specific ω from a parameter \mathbf{A} different from the specific α .

This also means that ω is a candidate to the *central parameter* which should be interpreted as an interaction of a parameter specific for the individual fish and a parameter for the specific type of activity and environment, and this is in fact what is done in Iven's monograph and in his dissertation (1970), where ω is analyzed as a product of independent multiplicative factors.

However, from a physical perspective, respecting dimensionality of parameters, ω with the dimension 'time raised to the potency -1.513' can't be split in multiplicative factors with that same dimension. If ω is going to be factorized it should rather be multiplied with dimensionless factors. But that breaks the symmetry aimed at between the individual and the activity/environment factors.

Perhaps this difficulty points to the fact that no arguments are given why the 'components' in ω should be multiplicative factors. They could as well be additive, which on the one hand would solve the dimension problem, and on the other hand would also be more in accordance with Rasch's general concept of 'specific objectivity' based on 'latent additivity', where the exponential function in the expressions for probability transforms addition to multiplication.

Unfortunately this possibility is not at play in the works mentioned.

Arguments against the \mathbf{A} and ω (or α and λ) model and for the \mathbf{A} (or α) and τ (or ϑ) model and suggestions for a possible future re-interpretation of the data or new experiments (leaving out the problems with estimation of a specific ω from a parameter \mathbf{A} different from the specific α):

But still this possible explanatory role of the parameter ω is no sufficient argument for also letting ω define the basic form of the model. The arguments for choosing ϑ or τ , together with \mathbf{A} (or α), in the basic descriptive model, to make it transparent, easy to estimate, and easy to communicate, are still weighting more. Furthermore, there is no problem in calculating the derived parameter ω from the basic descriptive ones, and the individual parameters and the milieu parameters could as easily be estimated with the \mathbf{A} (or α) and τ (or ϑ) model.

Letting ω define the basic *descriptive* model is also a way of *a priori* closing the field of possible *explanatory* parameters. You could as well point to ϑ or τ as central explanatory parameters as expressions of how long *time* it takes to reach a certain level in the intensity function, referring to a ‘biological clock’ in the fish. Even more obvious you could point to the parameters $1/\vartheta$ or $1/\tau$ as expressions of the ‘speed’ of the biological clock, *e.g.* how much the fish ‘opens the sources to fill the motivational vessel’ before reaching the threshold of action or end of action. Here a simple additive structure of the parameter-components would further be obvious. In fact, when looking at the generalized Poisson-process for number of events in a fixed interval of observation, ‘reciprocal’ to the waiting-time model, $1/\vartheta$ or $1/\tau$ will be the basic additive *rate* parameter.

Further, a *hypothetical physiological model* for ‘how the motivational vessel is filled’ with the passage of time could even be suggested on these grounds. The pressure in a tissue with cylindrical elastic vessels being filled with fluid in a constant speed raises approximately proportional with the square root of time, or $\text{time}^{0.5}$. This is also how the intensity function develops in time if α is set to be \mathbf{A} , as $\mathbf{A}-1 = 0.513$ which is very close to 0.5. The empirical α ’s are different from \mathbf{A} . But this possible ‘base line’ could perhaps be used in a discussion of α ’s variations.

This is not to say that this will turn out to be the final solution to the problems. Other choices of derived explanatory parameters may be possible, and could be tested empirically. But there is no reason to exclude this field of hypothetical explanations *a priori*, which Iven and I felt Rasch did.

The reliable raw data are still available in the *Appendices 1-5* (Reventlow, 1970, pp. 206-213), and it should be possible to re-analyze them with the methods suggested here, the general approach in the investigation is still valid, and the conclusions may still be far-reaching.

v Only recently, when preparing this postscript, I learned that this rare defeat on home ground could be a reason why Rasch never since referred to his co-operation with Iven Reventlow. Already in his opposition *non-officio* at the public defense Rasch in fact criticized his own methods and tried to make Reventlow responsible (see the editors' picture caption at the end of my above *Commentary*, 1986). This episode may perhaps also have contributed to the strange silencing of Rasch in the *Festschrift*.

vi In some other contexts, *e.g.* within mechanics or medicine, not involving temporal data, a model equivalent with Rasch's model with the parameters λ and α (or equivalent notations) may also be referred to as a Weibull-distribution and can be transformed to the model with the parameters τ (or ϑ) and α which is standard when describing *time-processes* with τ (or ϑ) as *time-scale parameter*. In the present paper about time-processes, especially 'waiting times', the term "Weibull distribution" is only used for a model with a time-scale parameter, *i.e.* not including Rasch's model (cf. Voetmann Christiansen, 1986, p. 39).

vii Damgaard Petersen does not refer to the explicit formula for the Weibull-distribution, as Voetmann Christiansen (1986, p. 39) does, but he uses the time-scale parameter τ in his re-analysis of Reventlow's data (Damgaard Petersen, 1986a) referring to the Weibull-distribution. Surprisingly, he identifies τ with the mean of the "waiting times", pointing to an unpublished student thesis. This is, however, only justified when $\alpha = 1$, see above p. 97.

viii It should be added that I personally always was on very good terms with Rasch, even when disagreeing, perhaps because I used his own arguments against him. He was also overtly impressed, and deeply dependent, by my programming and computational skills which were scarce at that time - to student discount wage. I enjoyed Rasch's wit, humor and anecdotes, besides learning a lot. I read nearly everything he had written and participated in his study groups and in Nordic Summer University's sessions on Rasch's psychometric methods, etc. I don't hesitate to call myself one of his pupils. I even have a correspondence with him (handwritten from his side) 1973-1977 about a generalization of his concept of specific objectivity to non-parametric domains (Mammen, 2008). Rasch was also very open about his early life which to some degree explained some of his 'darker sides'.

Methodological Envoi: A Few Guide-Lines (2018)

By Jens Mammen and Arne Friemuth Petersen

After this ‘*grausame Salbe*’, as Iven Reventlow no doubt would have called the above critical examination and refutation of the model he had been obliged to use when treating the results of his experiments, some guidance may be necessary for future users of his now restored ethological-statistical methodology, should they wish to decipher the contributions to their obtained results from the participating, individual animals, and respectively, from the environmental situations encountered by the animals.

To understand why Iven Reventlow’s investigation into the behaviour of sticklebacks, despite the problems hinted at above, was – and probably still is – a substantial innovative and important contribution to experimental ethology, and the study of behaviour in general, we shall emphasize some central elements in Reventlow’s method of analysis:

1. Traditionally, experimental ethology studying animal motivational systems and hierarchical structures using measurements of time – here exemplified by the study of sticklebacks – has used as data observed distributions of time of specific behavioural types and specific environmental conditions, on a group basis, to obtain sufficient significance when *comparing* these behavioural types and conditions using averages and dispersions for statistical comparison. This has brought about many valuable results, as seen in the rich ethological literature.

But when it comes to interpret these results in terms of dynamic temporal *development* of motivation *within* the individual animal this method of comparison is obviously insufficient. Standard methods assume implicitly that the observed measures of time follow a normal distribution, and accordingly that the motivational tendency to stop an ongoing behaviour at any moment (in statistical terms the distribution’s *intensity function*) occurs in a way specific for the nor-

mal distribution. If this is not the case – or, in fact, very much *not* the case – you can in this way only get some superficial impression of the animals' motivation, but not sufficient to relate it to fundamental biological mechanisms *in the individual*. This was the basis for Reventlow's wish to find a more realistic and reliable model for the temporal pattern in the individual fish's behaviour. Here Reventlow's collaboration with his statistical consultant, Georg Rasch, at the outset, was very fruitful.

Rasch proposed a two-parameter-model, a generalized 'waiting-time' model which, on the one hand, was based on biologically reasonable hypotheses about the temporal development of motivation in the animals (the intensity function) and, on the other hand, turned out to be much more fit with the experimental data than the normal distribution hypothesis.

At the same time as this model described what happened *within* each individual, it could, as well as the normal distribution model, be used for *comparisons* between individuals, types of behaviour, and environmental situations. There is no doubt that this was a substantial improvement of methods in experimental ethology.

2. Secondly, it was Reventlow's ambition to understand the interaction between the *individual* fish's motivational dispositions and the stimulating, or inhibitory, effects of the *specific* situations on a *dynamic* level, which could be related to the new deeper understanding of the *temporal development* of motivation described above. Traditional analyses of interaction had been accomplished by taking averages over observed situations and, respectively, over different individuals. However, Reventlow wished to analyse the data with a model of how the *individual* motivational tendency and the *specific* environmental influence *interacted dynamically*. Again, the inspiration from Rasch's work was indispensable. This was exactly what Rasch himself had successfully developed with his concept of *specific objectivity* and its practical implementation (see, above, Rasch, 1960), and for what Rasch later attained world fame in statistics.

3. These two virtues should be sufficient to justify a resumption and continuation of Reventlow's investigations and methods in experimental ethology. However, when implementing Rasch's two-parameter model something went wrong. Rasch insisted to use an unsuited version of the model, despite well-founded protests, as documented above. However, it is not too late to repair it, and the raw data are still available.

The three versions of the two-parameter model in equation (2b) in the above *Commentary* (p. 97) are empirically equivalent in the sense, that they describe the same observable distribution, and accordingly also fit the data equally well. The first version is here referred to as 'the Rasch model', the two last ones as 'the Weibull-models', although the third version is a slightly modified Weibull-model, inspired from models in physics, and with some interpretative and practical advantages.

Much of the above *Commentary* (1986) and the *Postscript* (2018) focus on the serious problems using Rasch's version, its strange fate in the scientific milieu, and the subsequent also strange silencing of possible underlying personal conflicts. Most dramatic, however, Rasch's model forced Reventlow to drop the principle of individuality of parameters and use a population average (**A**) of one of the parameters (α). This was both against Reventlow's ideals and intuition and against Rasch's own principles. Besides, the arguments for the parameter **A** were flawed.

This should, however, not overshadow the fact that the whole approach as such is still a methodological milestone, and when just using one of the Weibull-versions of the model instead of Rasch's version the problems should be surmounted. As to the practical implementation of the Weibull-models we can refer to the long *Note (iv)* to the *Postscript*.

Editorial Note (2018)

Simultaneously with Professor Rasch's Study Circle 1967-68, where he openly expressed his appreciation of the contributions from the participating psychologists, Reventlow was writing up an account of his experiments based on calculations of the time-measurements of stickleback behaviour, as related in the above *Preface* and *Commentary*. This manuscript was then tentatively translated into English in 1967-68 and retyped, up to page 40, on a 'flexo-writer' by the present editor, and the remaining 45 pages on typewriters by others, and thus terminated in monograph form by the end of 1968.

During this work Reventlow decided to write a doctoral dissertation based upon the same experiments, but enlarged with a Part II on methodology for studying non-reducible, psychobiological phenomena in humans, using the design of Rasch, and including new experiments carried out together with linguists Ingvar Holm and Cay Dollerup. The monograph left behind therefore represents Reventlow's first and fresh attempt at presenting the results of his experimental work with sticklebacks and the fruits of his collaboration with Georg Rasch during their five-year struggle to develop a suitable model of measurement capable of describing quantitatively the behaviour of the fish - a methodological achievement, which is here made accessible to international research for the first time.

When two years later, on April 14th 1970, Reventlow defended his dissertation, '*Studies on Complex Psychobiological Phenomena*', a palpable change had occurred in his relationship with Rasch. Even the journalists present could not help noticing it and described how a jovial atmosphere began spreading in the auditorium, when Reventlow, as candidate for the doctorate, declared that he had forgotten how the statistical calculations, which he had once understood, were to be carried out. Reventlow later told me, that he had felt obliged to pretend this slip of memory in order to avoid a fierce attack from his former advisor, Georg Rasch, who had asked him to write out some statistical technicalities on the blackboard for immediate and fatal dissection. The above *Commentary* and *Postscript* explore some possible sources of this disagreement.

When reverting to work on Reventlow's monograph I was conscious of embarking on a project that might have one or two odd problems of method unresolved, but I had not imagined that their solution, thanks to Professor Jens Mammen's contribution, would lead to the final breakthrough every one of us had hoped for fifty years ago. Nor did I expect that the history of the project would hold a scientific thriller, which has only been brought to light, but not yet explained, by his critical analysis of the employed statistical model.

The present manuscript, then, consists of a thorough revision of the first 9 sections of the 1967-translation of Reventlow's monograph followed by the Sections 10-13 that contain the corresponding, and definitive, paragraphs from his dissertation. A part of the editorial work consisted in making the monograph version tally with the dissertation's more detailed interpretation and discussion of the results. The data presented in *Tables 1-5* are extracts from the entire data collection, printed in the *Appendix* to the dissertation on pp. 206-213. An appropriate title to indicate more precisely than the original title, '*Psychological Analysis of Behaviour by Means of Statistical-Ethological Studies of Fish*', what is achieved in the monograph has hopefully been found, and a few references supplied and corrected. The *Commentary* by Jens Mammen was first published in Danish in 1986 and the added *Postscript* written for this publication, as related by the Author.

At journey's end, I extend my cordial thanks to Jens Mammen for his readiness to resume the collaboration we had begun in the 1960s as assistants to Iven Reventlow, in order to bring out our professor's unpublished work which, with the now completed methodology, arrives at solving the fundamental psychobiological problem it originally addressed. Without Jens Mammen's meticulous analysis of the applied statistics and his contribution of a new, tenable mathematical model, this monograph could never have taken the form of a guide for future students of behaviour.

We are much indebted to two anonymous reviewers for their evaluation of the manuscript and their helpful suggestions, and to dr.phil. Marita Akhøj Nielsen, Editor in Chief, for a pleasant col-

laboration on the arrangement of the book, and for her successful search in the Academy Archive. For editorial assistance I am indebted to translator Teresa Sawyers for her edits to the translation of Reventlow's text. Last, but not least, my cordial thanks go to Countess Ida Reventlow for granting me permission to work on and complete the translation of her husband's manuscript with a view to publication.

Arne Friemuth Petersen

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