ASPECTS OF THE BEHAVIOURAL ECOLOGY OF THE SHAG *PHALACROCORAX ARISTOTELIS*

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I hereby declare that I alone wrote this thesis, that it reports my own work, and that it has not been submitted in part, in parts, or entirety, in any previous application for a higher degree.

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June 1988

ABSTRACT

This study was concerned with various aspects of the behavioral ecology of the Shag. The main findings were as follows.

An examination of monitoring methods for the Shag confirmed that early June is the best time to make a count, regardless of the date of onset of laying.

The project was largely concerned with the feeding behaviour and diet of the Shag. Time of feeding was found to be related to time of day, the number of feeds given to chicks reaching a maximum 3.5 hours after sunrise. There was no relationship between the brood size and the number of feeds given to chicks, or between brood size and growth. Diet was found to consist almost entirely of sandeels.

The time budget of the Shag at the nest-site was estimated. Six categories of behaviour accounted for most of the time budget. None of these categories showed a difference due to sex.

ACKNOWLEDGMENTS

I am indebted to the following people for data, expertise and assistance freely given to me during the course of my research: Nicholas Aebischer, Pete Ewins, Jimmy Gauld, Jeff Graves, Mike Harris, Andrew Russell, Sheila Russell, Peter Slater, and Sarah Wanless.

I am grateful to Pat Cooper, who typed the captions for the figures, to the various lighthouse crews who transported equipment and supplies across the island, and to the boatmen of Crail and Anstruther, in particular Jimmy Smith. Finally, I would like to thank Sharon Forbes, who retyped the manuscript and typed the growth data for appendix B.

1 INTRODUCTION

The behaviour of the Shag has been well documented (Snow, 1960,1963), though not in quantitative terms. There is very little information on how the Shag divides up its time between its various activities, and also very little information on how the two sexes divide the responsibilities of producing and raising offspring.

The work which follows falls under three main headings, each of which is introduced and described below, along with an outline of the aims of the study.

1.1 Monitoring Methods

Seabird numbers can act as a sensitive indicator of changes in the sea. For example, changes in the numbers of prey can affect numbers of seabirds (Brown, 1980), and it is important that accurate and reliable techniques be developed to monitor seabird numbers. The figure generally taken to represent an index of the breeding population of Shags is the number of nests counted in early June (Potts, 1969). The purpose of this part of the study was to assess the reliability of a count at this time, in view of the fact that the date of the first egg for the Shag is extremely variable (Aebischer, 1985).

The study area used in this project contained around 290 nests which were easily visible from vantage points, without it being necessary to actually enter the areas where the nests had been built. This was an ideal situation for the purpose of assessing a monitoring technique.

The area was mapped, using both sketch maps and photographs, in April

1986. This meant that the nest sites could not only be accurately located, but changes in occupancy (abandonment of sites, and the use of new sites) could be accurately recorded. With this accurate mapping, independent counts could then be assessed in the light of knowledge of the exact number of pairs that had nests, or were starting nests at any particular time.

1.2 Feeding Biology

The central theme of this study was the investigation of the feeding biology of the Shag on the Isle of May. There were two aspects to this, namely feeding behaviour and the composition of the diet.

1.2.1 Feeding Behaviour

Very little work has been done on the feeding behaviour of the Shag. Snow (1963) looked at the feeding of Shag chicks on Lundy, and described the behaviours involved as well as making some quantitative assessments, though with very small sample sizes, and the use of a somewhat arbitrary definition of what constitutes a feed. There is considerable variation in behaviour between different pairs, and results based on just one or two nests must be treated with caution. To summarise briefly, Snow found an increase in feeding rate through the day, with very few feeds being given in the morning, the maximum feeding rate occurring two hours before sunset. She also noted possible sex differences in the feeding of chicks, with the female doing the bulk of the feeding of very young chicks.

Pearson (1968), working on the feeding biology of a number of species on the Farnes, looked at diet composition, feeding range, and the feeding and growth rates of chicks. He estimated a maximum feeding range for the Shag of 11.5 miles, based on their known flying speed and the length of time spent by birds away from the island on feeding trips. He said nothing about the locations or directions of the feeding grounds used, except to state that during the summer Shags, along with Eider ducks, could be seen fishing within sight of the islands. The feeding range he gives easily allows Shags from the Farnes to fish off the Northumberland coast.

Pearson's data on the growth rates of Shag chicks compared the growth of chicks from broods of one, two and three. Chicks from broods of three showed a slightly lower growth rate when compared with chicks from broods of one or two, although the difference was not statistically significant. Pearson felt that this could not be explained on the basis of food shortage, since Shags spent less than 10% of the daylight hours fishing, and thus did not appear to be stressed for food.

Snow (1960), in an earlier paper, also presented growth rate data, giving a composite growth curve, and also a growth curve comparing first, second and third hatched chicks, based however on only one nest. From the linear part of her composite growth curve (Figure 1, p569) it is possible to estimate a mean daily weight increase of about 47g/day, which is comparable to the values for daily weight increase given by Pearson (1968).

The aim of the present study was to describe the feeding behaviour of the Shag on the Isle of May, and to relate the rate of feeding of chicks, and the number of feeds given, to their growth rate. The timing of feeding and the factors (tidal or diurnal) influencing this were examined, along with the relationship between brood size and feeding frequency. Growth rates were recorded from repeated measures taken from a sample of chicks from broods of different sizes, to examine the effect of brood size. Finally, some indication was sought of the location of the feeding sites, and of the feeding range of the birds.

1.2.2 Diet Composition

Several studies have concentrated on the composition of the diet of the Shag. The first major study was that carried out by Steven (1933), based on the analysis of stomach contents of Shags destroyed as a suspected threat to commercial fish stocks. He found that commercially valuable fish were by no means a significant feature in Shag diet, and that Shags depended largely on sandeels (*Ammodytes spp*).

Subsequent studies have also found sandeels to be an important constituent of Shag diet (Lumsden and Haddow, 1946; Snow, 1960: Pearson, 1968), though one study (Mills, 1969) found gadoids and herring to be more important. The exact composition of the diet varies according to locality, a fact which probably depends on local fish populations. Lumsden and Haddow (1946) presented data showing that diet composition varied according to the character of the sea bed at the place where the birds were shot, suggesting that the nature of the sea bed in a particular locality determines the type of fish to be found there.

The present study represents the first study of the diet of Shags breeding within the Firth of Forth. Feeding conditions around the May are currently very favourable for seabirds (Harris, 1985), so the data presented here also represent a description of the diet of Shags which are not stressed as a result of an inadequate food supply.

This study is also the first to be based almost entirely on an analysis of pellets. Shag pellets have previously been described only by Snow (1960), who gathered a few, and looked at their contents. This omission is surprising, since the existence of pellets is well known in related species (Van Dobben, 1952; Mills, 1969b; Duffy and Laurenson, 1983).

Pellets provide an extremely useful means of looking at the diet of the Shag, since their use does not require either the disturbance necessary to obtain regurgitates, nor the removal of individuals from the population. Very large samples may easily be gathered , and repeated sampling may be carried out in the same area, allowing the analysis of diet throughout the year, based on the same population.

1.3 Time Budgets

Time budget data has been collected from a number of species (eg Orians, 1961; Custer and Pitelka, 1972; Utter and LeFebvre, 1973; Weathers and Nagy, 1980; Williams and Nagy, 1984; Bernstein and Maxson, 1985), though with the exception of Bernstein and Maxson's study, seabirds have been largely ignored.

Examination of the time budget provides an insight into the way the animal divides up its time, and can provide a basis for answering questions about changes in activity patterns throughout the year, and the division of time between the sexes. Bernstein and Maxson (1985) produced a time budget estimate for the Blue-eyed Shag, based on direct observations and time-lapse photography.

Their data suggested that males incubated more than did females, though the adults appeared to feed the chicks with equal frequency once they had hatched. Females appeared to spend more time foraging during the brooding period compared to males. Throughout the brooding period, there was always one parent present at the nest, probably as protection against Skuas.

The aim of the present study was to produce a time budget for the Shag on the Isle of May during the breeding season. This was restricted to activity at the nest site, due to the problems involved in observing the birds once they had left the nest.

The time budget was produced with two questions in mind: How does the time budget vary through the breeding season? and How does the time budget differ between the sexes?

2 STUDY SITE AND GENERAL METHODS

2.1 The Isle Of May

This study was carried out on the Isle of May, which lies in the mouth of the Firth of Forth, about five and a half miles off the Fife coast. The Isle of May has an area of about 140 acres, with steep cliffs on the west and south west sides, from which the ground slopes down to sea level on the east side.

Altogether, 91 days were spent on the island in 1985, and 101 days in 1986. In addition to periods of continuous occupancy, two day-trips were made in June of 1985, when it was impossible to obtain accommodation on the island. Samples of early-season pellets were collected during two overnight visits in January and February 1986.

2.2 Study Area

The main study area was located at the South end of the island and comprised an area of low cliffs on which around 300 Shag nest sites have been counted (*pers obs*). A hide was erected early in each season opposite a sub-colony of 20-25 nest sites in which every breeding bird has been individually colour-ringed since 1983. All of the observational parts of this study were carried out on these birds.

2.3 The Shag On The Isle Of May

The Shag was first recorded as breeding on the Isle of May in the 1820s, when "a few pairs" were recorded (Eggeling, 1985). In 1918, one pair was recorded as breeding, and 2 pairs were recorded in 1924. By 1934 at least 6 pairs were breeding, and numbers have continued to increase since then, to their present level of around 1300 pairs attempting breeding each year (S Wanless, pers. comm.).

The birds on which the present study was made have been studied since 1984 by Dr J A Graves (University of St Andrews), and records of fledging success are available since then, and also behavioral data from the colour-marked area.

2.4 General Methods

2.4.1 Observational Methods

Much of this study is based on behavioral observations of the colour-marked birds. Observations were made from the hide, which was sited about 8m from the focal group on the opposite side of the gully in which the birds nested.

In the 1985 season, these observations were largely of behaviour, which was recorded onto cassette tape and later transcribed. Once chicks had hatched, a number of watches were done for the specific purpose of observing the feeding of chicks. These included two dawn to dusk watches.

In the 1986 season, some watches were done early in the season to obtain a record of the behaviour of the birds in the focal group, but for the most part the emphasis was on time-budget watches (see Chapter 6).

These were typically done in two hour blocks, staggered so as to cover dawn to dusk over three days. Observations were recorded on checksheets. Again, in 1986 feeding watches were carried out once chicks had hatched. These were also staggered to cover dawn to dusk over two or three days. Two dawn to dusk watches were carried out.

2.4.2 Pellet Collection

In January and February 1986 two overnight stays were made on the island for the purpose of collecting pellets. From March to August, pellets were collected over longer time periods. In the early part of the season pellets were collected once every three days to make up a sample of at least 30 for each month, but once chicks began to hatch pellets became much rarer in the breeding areas, and collection had to be more opportunistic.

2.4.3 Ringing

In 1985 all chicks in the study area were ringed, as were any unringed breeding adults that were caught. In 1986 all of the chicks in the focal area were ringed, and attempts were made to ring the chicks in the rest of the study area, although this was hampered by the presence of guillemot chicks on some of the cliffs. Entering these areas was impossible since it would have resulted in the premature departure from the cliffs of these chicks, with consequent mortality. As a result of the delay until the guillemots had fledged, some of the Shag chicks had fledged before they could be ringed.

Attempts were also made to catch and ring any unringed adults. In addition, around 100 adults were caught and colour-ringed in the study area as part of a project on population monitoring being carried out by Dr M P Harris (ITE, Banchory).

2.4.4 Growth Of Chicks

An area of around 30 nests in the study area, distinct from the focal group was used for repeat weighing of chicks. This area was excluded from other studies, such as colour ringing for the purpose of monitoring.

2.4.5 Monitoring

Nests were counted at intervals throughout most of the season. In addition to recording the number of nests, their locations were marked on photographs, and the size of the nest was recorded (categories used to estimate nest size are described in detail in Chapter 3). Two independent observers (M P Harris and S Wanless) also counted nests and recorded their sizes as part of the monitoring project.

3 THE EFFECT OF DATE ON COUNTS OF SHAG NESTS

3.1 Introduction

Shags *Phalacrocorax aristotelis* build large bulky nests which successful pairs occupy for some 16-17 weeks. Where the birds nest on open ledges, these nests are easily counted and a single annual count of nests during early June is often used as a measure of the size of a breeding population (Cramp, Bourne & Saunders, 1974). The timing is based on the work of Potts (1969) on the Farne Islands, Northumberland in 1963-67. The aims of this study were to confirm that this was the best time to make such counts at another colony 20 years later, and to check the accuracy of such counts by comparing them with counts obtained from a detailed survey of the area based on photographs.

3.2 Methods

Part of the nesting colony at the south end of the Isle of May NNR, Fife, where Shags nest on ledges on small cliffs and offshore stacks, was photographed in April 1986. Breeding density was high with 290 sites being occupied along 100m of coastline. As pairs started to breed, the position of each nest was marked on the photographs, a complete check of all nests being made approximately weekly from 12 May until 27 July 1986. Each nest was categorised as - (a) active, meaning that the nest was at least being defended by the adults, and may have produced eggs or young (identified by either bird sitting tight, whether or not eggs or young were seen or an unattended brood of young), (b) full nest (well built but seen to be empty although apparently capable of holding eggs), (c) half-built (platform of nest material but insufficient to hold eggs), or (d) trace (a few fragments of material guarded by one or both adults).

Active and full nests are the categories usually counted and combined together as 'nests' in widespread population censuses (eg Operation Seafarer, Seabird Colony Register). This check using photographs aimed to account for every nest present in that part of the colony which was being surveyed, and was necessarily more detailed than the census counts, since the object was to obtain a detailed knowledge of the area to provide a baseline against which to compare the census counts.

Approximately weekly Sarah Wanless and Mike Harris independently, both of myself and of each other, mimicked a typical census count and checked the whole area from all vantage points constrained only by the need not to disturb incubating birds, and categorised all the nests they saw as above.

These independent counts were then compared with each other, to gain a measure of the consistency of the observers. Finally, they were compared with the actual numbers of nests, derived from the photographic surveys. This gave a useful comparison between the count which might derive from a typical census, and the absolute numbers of birds present.

Since, by doing the photographic surveys, I developed a knowledge of the area which was far more detailed than would be the case in a normal census count, it was not felt that census counts made by me would truly reflect "typical" census counts.

Only nests with at least 1 adult (or a brood of young) present were counted. This criterion was necessary as an indicator that the nest was not abandoned. A nest, however large, which is unattended by at least one adult for any length of time is a sign that the adults there have abandoned their breeding attempt. Any unattended nest will quickly be destroyed by neighbours scavenging for nest material, and including such nests in counts will overestimate the number of breeding pairs present. When both S W and M P H made counts, the mean of the two counts is used as the count for the day. The comparisons between these counts and those from the weekly check of photography mapped nests were restricted to parts of the colony visible from these vantage points. The difference between counts made by two counters or by two methods is given as the mean and standard deviation of the individual differences between the two counts, always treating the same count first, divided by the average of the two counts.

3.3 Results

There was remarkably good agreement between the combined counts of active and full nests found by the counters and the checks of the area using photographs. On the seven dates where both methods were used the mean difference was only 1.4% (sd 6.8). Thus, it may be concluded that S W and M P H overlooked few nests and their counts are used throughout this chapter.

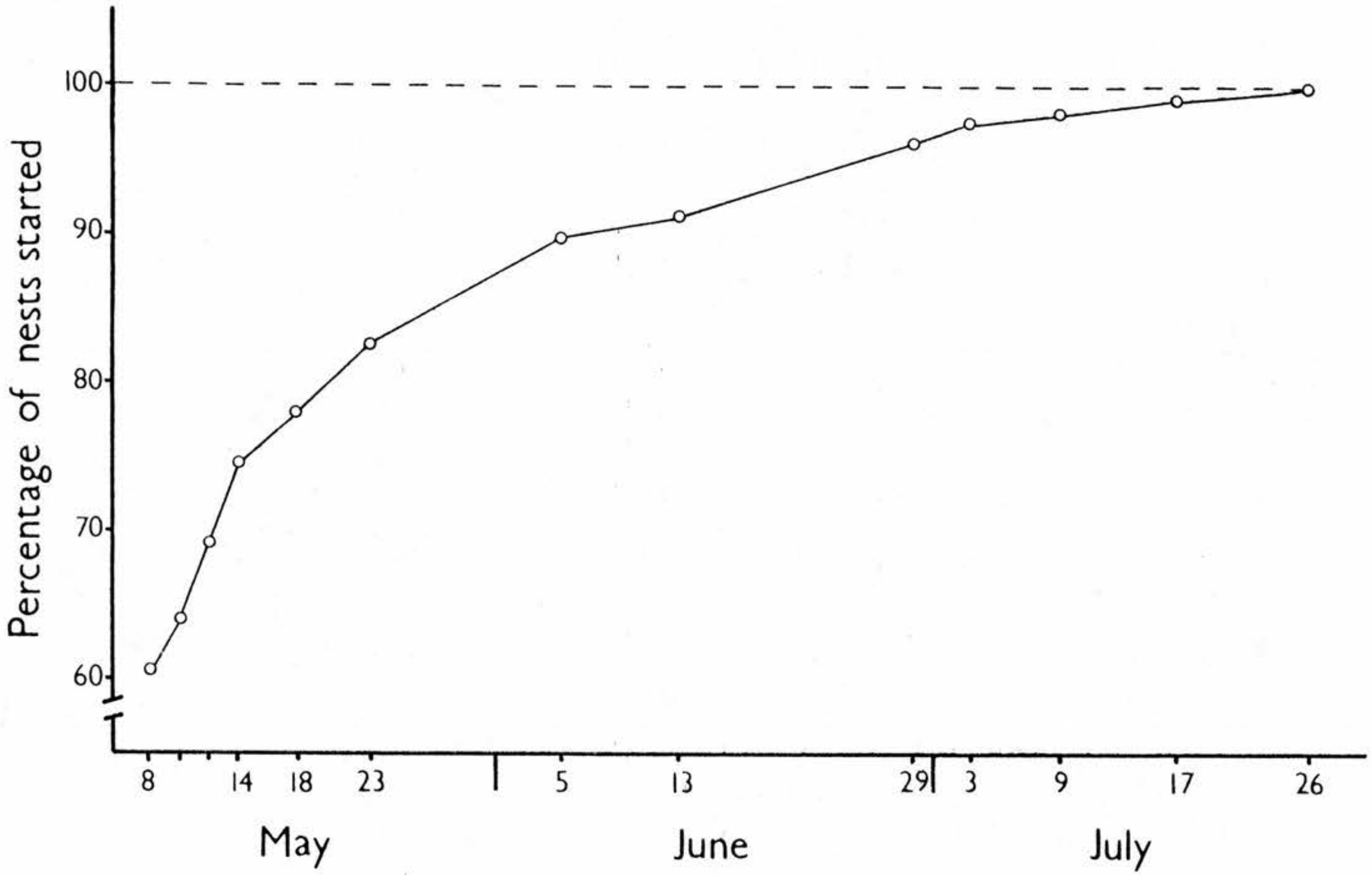
On the 8 days when S W and M P H made direct counts there was good agreement between their counts, the mean difference in the counts of active nests, expressed as a proportion of the higher count, being 2.3% (sd 3.1). There was, however, a difference of 15% (sd 33) in the combined counts of trace and half nests. This was thought to be due to (a) the difficulty of deciding when a pair started to build (eg whether a few pieces of seaweed had been brought there by the birds), and (b) pairs sometimes leaving the sites unattended at this stage. The mean difference in their total counts was 3.2% (sd 2.9).

Overall 290 different nest sites were used during the period. Over 90% of the sites used had had at least a trace of a nest by 13 June but 11 sites (4%) were not occupied for the first time until July (Fig 3.1). No nest was started after 27 July. Of these 290 sites, 252 (87%) reached the active stage, and a further 13 (5%) the full, 15 (5%) half and 6 (2%) had only a trace. Four nests (1%) were almost hidden from view so the state which they reached was unknown. Thirty sites were occupied on several different occasions and at 10 there were 2 successive active

Figure 3.1

The proportion of the 290 nest-sites used by Shags on the Isle of May in 1986 which had a nest started by a given date. Data are from checks using photographs to ensure that no sites were overlooked.

Figure 3.1


Percentage of nests started
100
90
80
70
60
8
14
18
23
5
13
29
3
9
17
26
May
June
July

sites. Five of the 30 sites were used by individually recognizable pairs. One was used by 2 different pairs, both which had active nests at that site some during the season, 3 were used by 2 different pairs but only 1 nest reached the full stage and 1 was used twice by the same pair. One male deserted his nest and 5 eggs about 10 June after being colour-ringed and moved 85km to the Farne Islands and bred again in the same season, successfully rearing one chick (P Hawkey pers. comm.). This movement must be considered exceptional because the individual concerned had apparently bred in the study area since at least 1971 and had been caught in 4 previous seasons. The number of pairs which actually bred in the area in 1986 was not counted, but the maximum number of pairs occupying sites on any day was 240 on 5 June.

The first egg on the island was seen on 4 May and the first in the study area 2 days later. From then on, nests were both started and disappeared (with the material being stolen by neighbouring pairs) throughout the period. The total number of active nests present increased to a peak of 224 (89% of the season's total) on 5 June (Fig 3.2) and then declined slowly but significantly. The relationship between date and number of nests was: No of nests = 229 - (0.86 x date), taking June 1 as day 1 and counting dates from that starting point ($r = -0.94$, $n = 9$, $P < 0.001$). The number of half built and trace nests showed a corresponding decline and remained at around 10. The peak count of the total number of nests was 237 (82% of all those recorded) and this also occurred on 5 June.

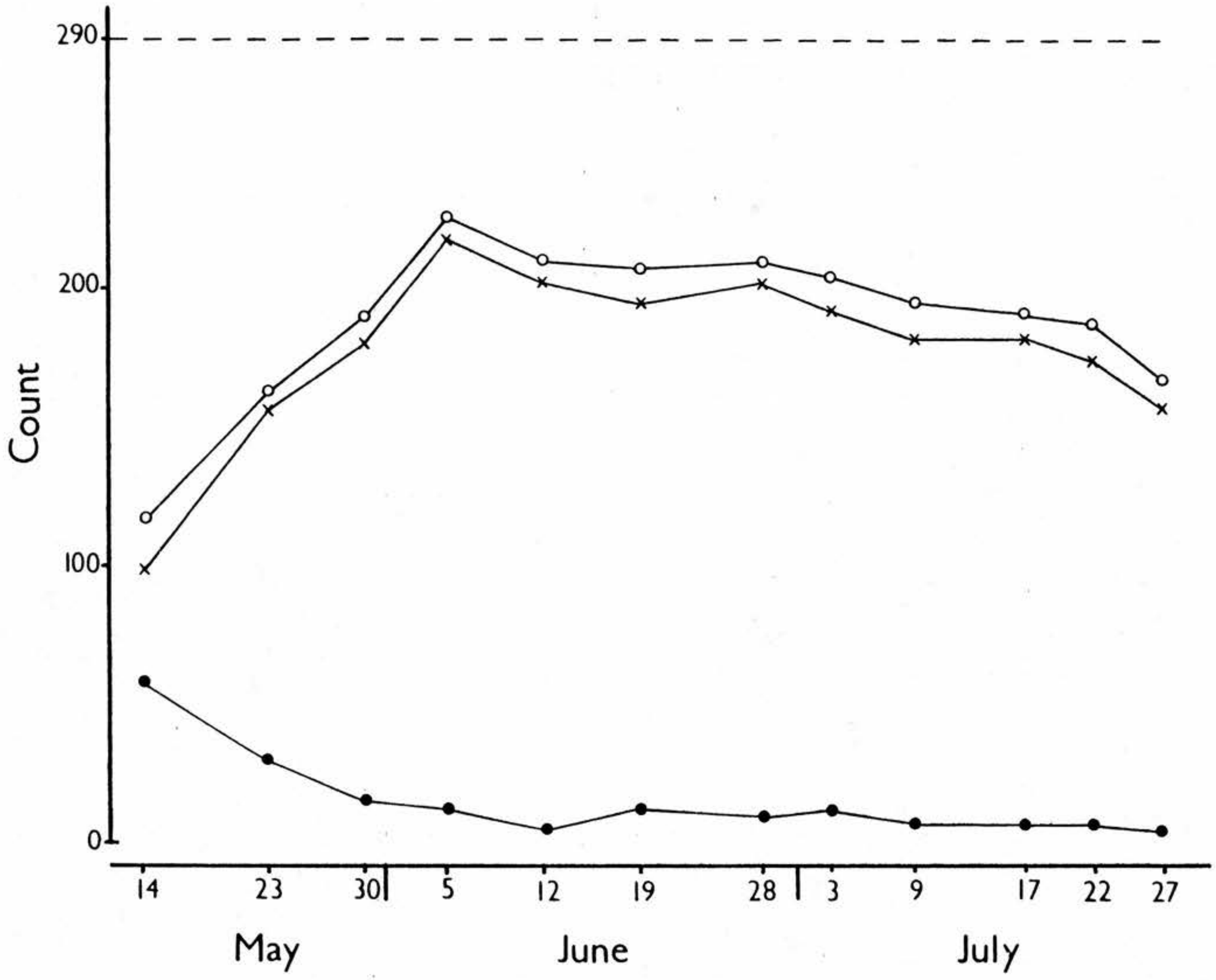
3.4 Discussion

On any one day some pairs will not have started breeding, others will have failed and left. Thus the maximum spot counts will underestimate the population. However, the total number of sites used during a season will overestimate the population as some birds change sites during the season. On the Farne Islands, where Shags also nest on open ledges, Potts, Coulson and Deans (1980) considered that the most accurate index

Figure 3.2

Counts of entire and full nests combined (o——o), active nests (x——x) and half-built and trace nests (●——●) in the study area in 1986. Data are from normal counts without using photographs. The decline in the number of nests in June and July is significant ($r = -0.94$, $P < 0.001$) and its mean rate was 0.86 nests per day (regression analysis).

Figure 3.2



of population size was the maximum numbers of nests occupied at any time. They expressed this nest count as breeding pairs, noting that each pair (as defined above) occupied 1.15 sites per season. Despite over 80% of the adults being individually recognizable (G R Potts pers. comm.) some unsuccessful pairs probably moved from site to site without being identified, so this ratio will underestimate the number of sites being used by more than one pair within a season. On the Isle of May in 1986, 290 sites had a nest at least started and the maximum number of sites occupied at one time was 240 (based on checks using photographs) - a ratio of 1.21 sites occupied per pair if, and this study presents no evidence to back this up, it is assumed that all pairs were actually nesting at one time. In 1982, Aebischer (1985) used photographs to check the whole of the Isle of May colony several times and found that 1916 sites had had a pair and at least a trace of a nest at some time during the season. His maximum spot count was 1733 nests, giving a ratio of 1.11. Ratios of this type will doubtless vary between colonies and G R Potts (pers. comm.) noted that they were higher in low quality nesting areas, eg where waves wash away nests.

A further source of inaccuracy in counts is the difficulty in actually seeing nests. This was not a problem in our area, but elsewhere on the Isle of May some Shags nests are hidden in caves and in fissures in the cliffs. Such nests are easily missed. Aebischer (1986) considered that 15% of all nests would have been overlooked during a normal nest-count. Counts of peak nest numbers are thus likely to under-estimate the population.

Census counts in Britain are usually made in early June following the findings of Potts (1969) on the Farne Islands that numbers of occupied nests tended to be highest then. The timing of breeding of Shags is extremely variable and this might be expected to influence the best date to make counts. There are few median laying dates but the first egg date on the Farne Islands for 15 seasons 1972-86 was 12 April (sd = 12 days) (Hawkey and Hickling, 1972-87). Start of laying on the Isle of May showed a similar annual variation with the first egg date for 20 seasons during the period 1962-86 being between 23 March and 20 May (mean = 21 April, sd = 18 days) (Aebischer, 1986, pers. obs.). Thus 1986 with the first egg on 4 May was a late season. The optimum time for a single count of the nests, that is the time when a maximum count is likely, on the Isle of May in each year 1981, 1982 and 1986 was the first third, even though the first egg dates in these years varied between 28 March - 4 May. In 1976, laying started on 20 May - one of the two latest dates on record (Aebischer 1986). On 2-4 June that year, H Galbraith (pers. comm.) counted 348 occupied nests on the Isle of May, whereas on 27-30 July M P H and others found 479. It would be interesting to have details of the nesting pattern in such a very late season. Subjectively, it seems that laying is more synchronised in late seasons. Thus care must be exercised in using counts made in June of very late seasons of which there have been three since our records began on the Isle of May in 1972. Laying patterns at other colonies should be checked before taking the first week of June as standard time throughout Britain. For, although the available evidence confirms the view of Potts *et al* (1980) that a single count of occupied nests at this time is normally a good index of the number of pairs breeding that year (even though its accuracy remains unknown), Shags breed much earlier in southwest Britain than they do in the northeast (Potts 1969, Table 3). Counts should perhaps be made earlier in these regions.

Occasionally, as shown by Aebischer (1986), large numbers of Shags fail to nest. In such seasons any count of nests will give a misleading indication of population size and will thus be inadequate on its own. Therefore any count of Shag nests should be supplemented by an objective assessment of whether there seemed to be far fewer nests than would have been expected from the numbers of adults present. For instance, annual counts of the number of pairs of Shags nesting on Canna, Inner Hebrides showed a dramatic increase between 1974 (856 nests) and 1985 (1690 nests). The count for 1986 was only 436 nests but over 1000 adults were counted on rocks close to the colony; obviously many pairs had not bred (details from Swan & Ramsay 1986). Such details are important to later workers when they need to compare counts. Aebischer (1986) showed convincingly the importance of having sufficient ringed birds in populations which are counted regularly to determine whether low nest counts do or do not reflect population declines. Adult Shags are now being colour-ringed on the Isle of May and at other Scottish colonies for just such a purpose.

4 FEEDING BEHAVIOUR

4.1 Introduction

The feeding behaviour of seabirds is of particular importance because they are often at the top of the food-chain and can thus be a sensitive indicator of changes, both natural and resulting from Man's activities, in the sea (Brown, 980). For example, Crawford and Shelton (1978) have linked the decline of a number of seabirds in South Africa to the decline of fish stocks due to overfishing, and the "red tides" around the Farnes in 1986 and 1975 (Potts *et al*, 1980) were accompanied by heavy mortality among Shags. Nelson (1978, p230) suggests that "man-induced changes in the food of gannets, and other seabirds, could be the most potent factor in future changes in their numbers and breeding biology".

In order that these problems may be identified, it is first necessary to have data on the species when it is not under such pressures. Conditions around the Isle of May seem to be close to ideal for seabirds at the moment (Harris, 1985), and many species, including the Shag, are currently increasing in numbers annually (Aebischer, 1985).

The data presented here were gathered during the 1986 breeding season. This season was one of the latest seasons, with respect to the date of the first egg, for which data exist (Aebischer, 1985), but was a normal season for chick production and the number of sites occupied.

4.2 Methods

4.2.1 Feeding Behaviour

The feeding behaviour of Shags was observed for 71 hours between 10 July and 4 August 1986. This was made up of two dawn to dusk watches carried out with the aid of Dr S Wanless, and an additional 36 hours of observation carried out in two hour blocks, staggered so as to cover dawn to dusk over three days. Two such three-day series of observations were carried out at an interval of one week. The two complete dawn to dusk watches were also separated by an interval of one week, and an interval of one week separated the second three-day series from the first all-day watch. An interval of one week is roughly equivalent to a shift in the tide of half a cycle. The watches were spaced in this way to enable tidal factors to be separated from diurnal factors. The weather conditions were similar during all watches, being characterised by prevailing westerly winds, good visibility, and little or no rain.

Observations were made of all birds in the colour-marked area which had chicks. This was a total of 14 nests, but was later reduced to 13 due to the loss of the chicks from one nest. Observations were recorded on cassette tape, and later transcribed. In addition, every 15 mins, a record of which birds were on each nest-site was made on a checksheet. This ensured that the attendance of the birds at the nest site could be estimated to the nearest 15 minutes, even if the time of leaving or arriving was missed. In addition, the sea rocks were scanned regularly for breeding birds, arriving or departing.

4.2.2 The Growth Of Chicks

Growth data were taken from a sample of 57 chicks from 26 nests in an area distinct from the focal colour-marked area. These chicks were weighed, and wing length measured, at intervals of 5 days, although adverse weather conditions occasionally prevented measurement on the scheduled day, so that a longer internal elapsed. Weights were recorded using spring balance, and were taken to the nearest 10g up to 1000g, and the to the nearest 50g for weights above 1000g. Wing length was measured to the nearest millimetre.

Eight broods lost a chick during the course of this study. In all but two cases this occurred when the chicks were very young, and for the purpose of this analysis the convention has been adopted that where a brood of size n has lost a chick, it is regarded as being a brood of size n-1 (Potts, 1966). The only exception to this was one brood of two which lost a chick aged about 32 days, which was found dead on the last day that weights were taken. This brood was regarded as being a brood of two.

4.3 Results

4.3.1 Time Of First Departure And Length Of Absence

Unlike most seabirds, Shags do not leave the colony at first light. During the four early watches, the earliest that a bird was seen to leave the island was 0314 GMT, which was 28 minutes after sunrise, and the latest time that the first departure was seen to occur was 0459 GMT, 101 minutes after sunrise.

Lengths of absence were recorded following the first departure during the two all-day watches. Length of first absence was felt to be of particular interest, because first thing in the morning the birds might reasonably be assumed to be empty of fish, and thus their first flight of the day is likely to be to a feeding area, to obtain fish for themselves and their chicks. Since it could only be stated with certainty that a bird had been feeding if it passed on food to a chick (Pearson, 1968), only those trips which were followed by a feed to a chick were included in the analysis. By determining the length of first absence from the colony, a mean maximum feeding range was estimated (assuming zero time spent fishing at the end of the flight).

The mean length of first absence for males was 31.6 mins, and for females was 28.4 mins. The difference between these values was not significant ($F = 0.13$, $p = 0.73$). The data for males and females were combined to give a mean length of absence of 30.0 mins. The mean flying speed of a Shag was assumed to be 30 mph (Pearson, 1968), giving a mean maximum feeding range of 7.5 miles.

4.3.2 Timing Of Feeding Of Chicks

A feed was defined as occurring when a chick inserted it head into the parent's bill. This definition differs somewhat from that of Snow (1963) and Pearson (1968); the reasons for this are treated in the discussion. Very short feeds (c 1-2s) were discounted from analysis, since it is doubtful if food was passed to the chick during these. This was the best criterion which could be used, since swallowing by the chick was rarely seen, particularly in the case of nests at more remote locations relative to the hide, and was never seem in very small chicks. In many of these very short feeds the chick either failed to insert its head into the adult's bill, or did not insert it fully. Although feeds were not timed, very short feeds were always identified as such by the observer. The timing of the feeding of chicks was examined in relation to both tide and time of day.

The two complete dawn to dusk watches were half a tide cycle different. For each day, the number of nests at which one or more feeds was given was determined for three-hour blocks centred on the high water mark, low water mark, or mid-point between the two (Fig 4.1). Corresponding periods with respect to tide were then matched. There was no significant difference between days ($F < 0.01$, $p > 0.50$), so data from the two days were combined to compare different states of the tide. No significant differences were found in the number of nests at which a feed was given between the different stages of the tide ($F = 3.67$, $p = 0.10$).

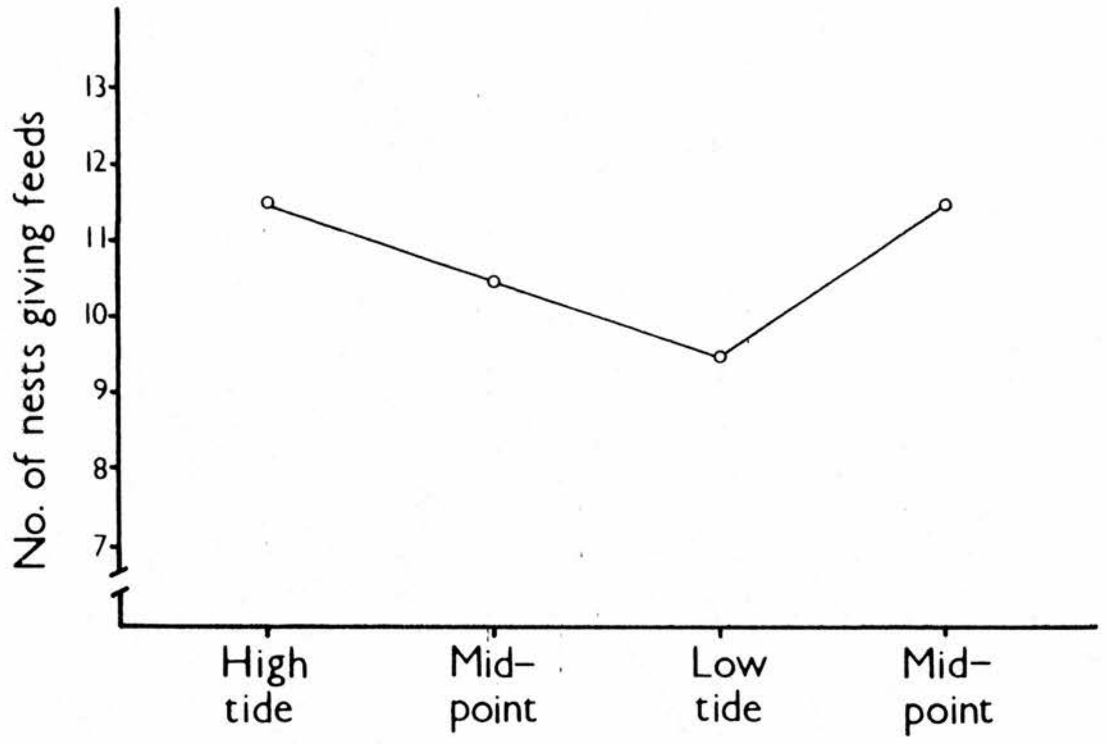
The number of nests at which feeds were given was also determined, from the two continuous watches, for one-hour blocks defined with respect to time from sunrise (Fig 4.2). The latest start began 27 minutes after time of sunrise, so the first hour block was defined as beginning 27 minutes after the time of sunrise. Corresponding one-hour blocks were then matched. There were 17 one-hour blocks from each day. There was no significant difference between days ($F = 0.03$, $p > 0.50$). There was a significant difference between hour-blocks ($F = 4.80$, $p < 0.01$), suggesting that time of feeding is dependent on time of day. This suggested that the staggered watches would give a picture of activity in the colony comparable to that obtained from the continuous watches for analyses based on time of day. Data from the staggered watches was thus also included in the analysis. The data from each three-day series of staggered watches were put together, and treated as representing a single continuous watch. Considering each three-day block as representing a single day, an analysis of variance found no significant difference between days in number of nests at which a feed was given for analyses based on time of day ($F = 0.23$, $p > 0.50$).

A significant difference was found between hour-blocks ($F = 5.01$, $p < 0.001$) and further analysis was carried out using the Scheffe Method, to determine which hour-blocks were significantly different with respect to the number of nests at which feed was given in that hour-block. The

Figure 4.1

The number of nests at which one or more feeds was given, analysed with respect to tide. Data are from two dawn to dusk watches which were half a tide cycle different (ie the time of high tide on one corresponded to the time of low tide on the other). Each point represents a three-hour block centred on either the time of high tide, the time of low tide, the midpoint between high and low tide following high tide, and the mid-point following low tide.

Figure 4.1


No. of nests giving feeds
13
12
11
10
9
8
7
High tide
Mid-point
Low tide
Mid-point

graph shows (Fig 4.2) that during the first three one-hour blocks and the last one-hour block fewer nests gave feeds. This was confirmed by the Scheffe test.

During the four early watches, the earliest that a chick was seen to be fed was 0441 GMT, 122 minutes after sunrise. This occurred during one of the two hour watches. During the all-day watches, the first feeds occurred at 0548 GMT, 150 minutes after sunrise, on one day and 0609 GMT, 184 minutes after sunrise, on the other. Incoming adults sometimes fed their chicks immediately upon return to the colony, but often waited for periods of up to 72.0 minutes.

Many birds did not feed their chicks after returning from their first absence of the day. The interval between the return to the colony and feeding a chick was determined for those birds which did feed their chicks on returning from their first absence of the day. This was a sample of 5 males and 5 females. When the time of departure and/or return of a bird was not known exactly, the midpoint between the minimum and maximum intervals was taken. The mean interval was 22.1 ± 26.2 minutes for males, and 14.4 ± 17.5 minutes for females. The difference between the sexes was not significant ($F = 0.68$, $p > 0.10$).

4.3.3 Number Of Feeds Given In Relation To Brood Size

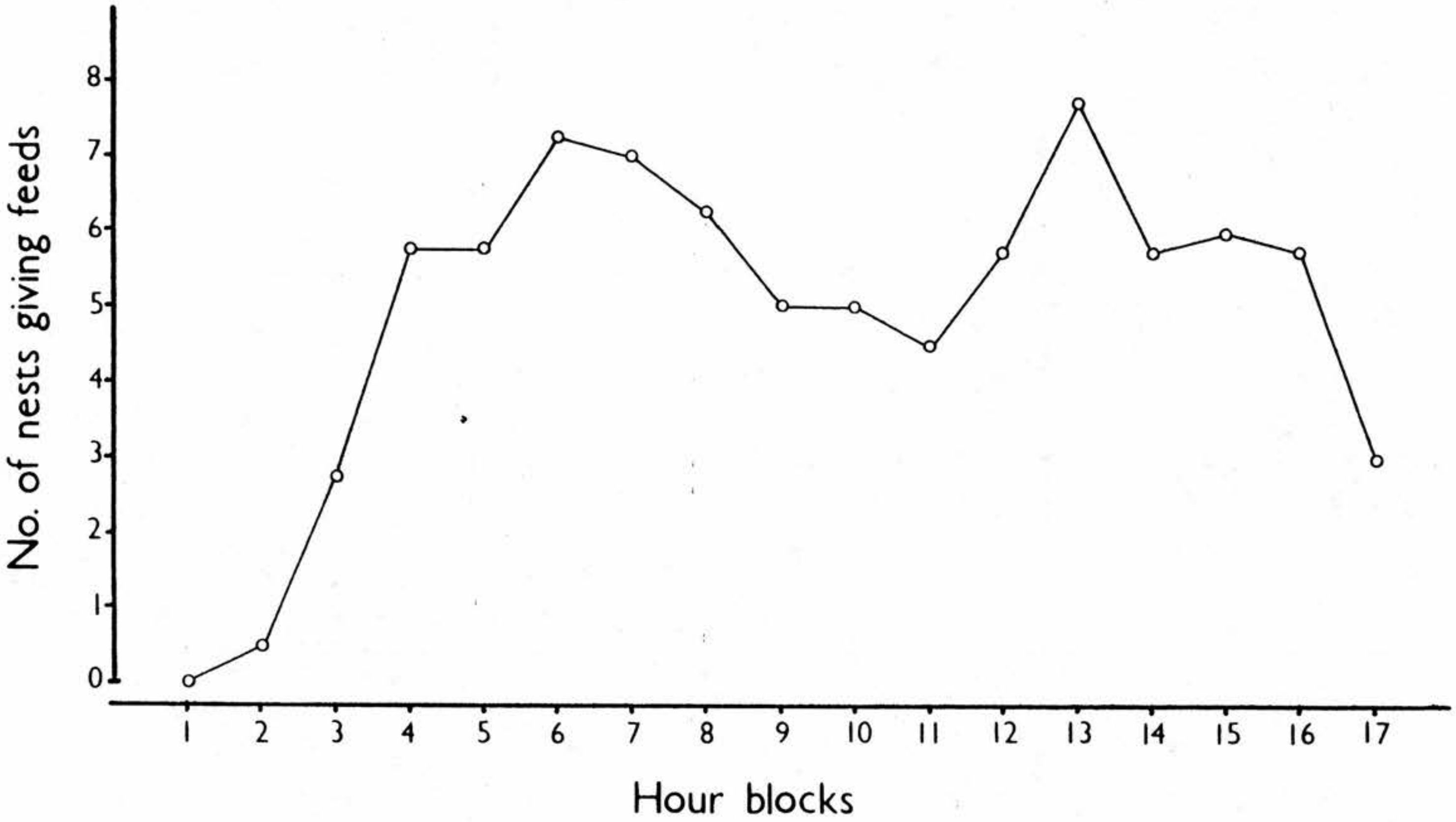
From the two all-days watches, the number of feeds given to broods of different sizes was determined. Altogether, there were 13 nests in the focal area which produced young and reared them successfully, but two of these nests were excluded from this analysis because the chick from one of them moved onto the other, and was fed by both sets of parents, creating a confounding influence.

For the remaining 11 nests, the total number of feeds given during each day was counted with nests grouped according to brood size. The mean

Figure 4.2

The number of nests at which one or more feeds was given analysed with respect to time since sunrise. Data are from two dawn to dusk watches, and two three-day series of watches staggered to cover dawn to dusk. Each point represents a one-hour block defined with respect to time of sunrise. The first hour-block begins 27 minutes after sunrise.

Figure 4.2


No. of nests giving feeds
0
1
2
3
4
5
6
7
8
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Hour blocks

number of feeds/day given to broods of various sizes was as follows:

BROOD SIZE	TOTAL NUMBER OF FEEDS/DAY	NUMBER OF NESTS
1	6.9	4
2	10.5	2
3	12.5	5

With analysis of variance no difference was found between days (F = 0.23, p > 0.10), or brood sizes, although the difference due to brood size tended towards significance (F = 3.30, p = 0.06).

4.3.4 The Growth Of Chicks

Hatching dates were known for only a few of the chicks, and as a result weight increase could not be related to age. However, Pearson (1968) identified the section of the growth curve between 400 and 1400g as linear and so was able to compare daily weight increase (DWI) over this part of the curve. Thus, in the present study, this section of the growth curve was assumed to be linear, and all analysis was based on this section.

This analysis was based on 7 broods of 1 chick, 12 broods of 2 chicks, and 5 broods of 3 chicks, including broods which lost chicks as described above. The remaining two nests were not used in this analysis, because in both cases the chicks were still very small at the end of the study, and their weights did not reach levels on which the analysis is based.

Best fitting straight lines were calculated for the part of the growth curves between 400g and 1400g, using the method of least squares. The daily weight increase for each chick was determined in this way, and mean daily weight increase for each brood size was compared by analysis of variance. The mean daily weight increase was as follows:

BROOD SIZE	MEAN DWI	NUMBER OF BROODS
1	45.69	7
2	50.72	12
3	46.74	5

There was no significant difference between brood sizes ($F = 2.16$, $p = 0.13$).

4.4 Discussion

4.4.1 Time Of First Departure And Length Of First Absence

Adults did not appear to leave the colony before sunrise. Counts made of the numbers of birds on each nest site in the colour-marked area at dusk and the following dawn were always very similar, suggesting that very little movement occurred at night.

The birds began to leave the island some time after sunrise, and were away on average for half an hour. It is important to note that the time of departure was not influenced by the state of the tide, and the pattern of attendance was similar in all watches, although the tides were different during each. No pattern of attendance dependent on tide, such as that found by Slater (1976) for the Guillemot (*Uria aalge*), was found. Interestingly, Sharp (1979), working on the attendance of Shags on the Isle of May in early April, described the time of departure as being related to the tide. However, his results are based on data collected during 6 consecutive days, during which time the tide would not shift enough to allow the separation of tidal and diurnal effects.

Upon return to the island some birds subsequently fed their chicks. Others went out to sea again, sometimes several times, before feeding their chicks. When leaving the island, Shags invariably flew North or North-west towards the Fife coast, and were never seen to head South from the island. The calculated mean maximum feeding range of 7.5 miles is sufficient to allow the birds to fish off the Fife coast, 5 miles distant. During a trip on a lobster-fishing boat on 6 September 1986, a number of Shags were observed fishing along the Fife coast between Crail and Kingsbarns. The Isle of May would be the nearest breeding colony for these birds. Earlier in the season, Shags were also observed fishing close in to the island, and on one occasion a group of Shags was observed fishing just off the West cliffs, presumably over a shoal of fish (King, 1972). These observations suggest that their preferred feeding grounds are in shallower waters (cf Rees (1965) who frequently observed Shags flying 8 miles between a roost site and a feeding site, which was a submarine ridge standing about 5 fathoms above the surrounding sea-bed).

Stonehouse (1967) reported similar findings for Pied Shags (*Phalacrocorax v varius*) and White-throated Shags (*P melanoleucos brevirostris*) in New Zealand. These species fished within 300m of the shore, flying to the coast from the roost site an hour or two after sunrise. Fishing stopped about an hour before sunset. Stonehouse suggested that good light was essential for visual hunting under water. This may depend on the nature of the prey, however. Shags may regularly be seen fishing in St Andrews harbour in very turbulent water when visibility under water must be extremely poor. Under these conditions they catch eels and flatfish (J Graves, *pers comm*). These are bottom-dwelling species, which the birds may be able to catch by feel, a method which they would not be able to employ when hunting free-swimming fish. N Upton (pers. comm.) has reported watching Shags swimming along just above the seabed, with the bill in the sandy bottom, catching fish buried in the sand.

4.4.2 Timing Of Feeding Of Chicks

The earliest that a chick was seen to be fed was 2 hours after sunrise.

Chicks often were required to wait much longer than this for their first feed of the day, although food-begging began before the first adult had left the colony, and even before sunrise on some occasions.

The number of nests at which chicks were fed rose to its maximum level during the first three and a half hours of the day, after which it remained constant throughout the day. This result differs from that of Snow (1963) who found a peak of feeding in the afternoon. Snow's study suffers from a very small sample size, being based on observations of only 2 nests. In addition, a feed is defined differently in this study. Snow defined a feed as being a series of head-insertions made within a limited period of time, whereas in this study a feed was defined as being a single head-insertion. This definition was adopted to avoid the problem of having an arbitrarily defined period of time to represent a feed. Chicks were observed to make head-insertions and to receive food from the same adult over quite considerable periods of time following the return of a bird to the nest-site. It then becomes problematic to define the end of one feed and the beginning of the next; The definition used in this study avoids this problem.

It is interesting to note that adults appeared to be able to resist the food-begging of their offspring for considerable periods of time. When an adult returned to the nest after having been absent for a while, it would be greeted by intense food-begging from the chicks, but might wait for up to 72 minutes before giving a feed. It is possible that an interval is necessary to allow digestion to take place, before the bird can regurgitate for its chicks. So far as could be determined, no studies of seabird feeding ecology have examined this possibility. As has been noted above, adults were also capable of remaining on the nest sometimes for several hours, before going out to feed, in spite of persistent food-begging from their chicks.

4.4.3 Number Of Feeds And Growth Rates In Relation To Brood Size

The number of feeds given to broods of different sizes was not significantly different, although the difference tended towards significance. It is likely that the result would become clear with larger sample sizes. Broods of 2 were particularly lacking. The present study was limited in this regard by the need to make a number of observations on a limited number of birds. Thus, the number of sites which were used for recording growth was kept to a minimum to minimise disruption.

If the suggested trend represents a genuine difference, then single chicks receive on average 6.9 feeds/day each, compared with 5.2 feeds/day each for chicks from broods of 2, and 4.2 feeds/day each for chicks from broods of 3.

It might be expected that this difference would be reflected in the growth rates, though the present study found no significant differences in growth between broods of 1, 2 and 3. Excluding broods of 1 from the analysis, the difference between broods of 2 and 3 tended towards significance.

It is possible that other factors are also at work here. For example, chicks from larger broods, while receiving fewer feeds, might receive larger feeds. The present study offers no data on this point.

Pearson (1968) found results similar to those of the present study insofar as he failed to find any significant difference in growth rates between broods of different sizes. His values for daily weight increase match very closely those obtained from the present study for broods of 2 and 3, but his figure for brood size 1 is 10g/day higher than that obtained here.

It was not possible to sex the chicks used in the growth study. Snow

(1960) sexed chicks by voice, and suggested that sex differences in weight become apparent after about 33 days; this is equivalent to a weight of around 1450g (from the growth curve presented in her paper). If this is a genuine effect, then the low weight of broods of 1 found in the present study cannot be explained in terms of a preponderance of females, since the weight difference due to sex should minimal for that section of the growth curve that was used for comparison (400g - 1400g).

It is interesting to note that Pearson's data shows a similar result in 1961. He presents data for 1 brood of 1, and 2 broods of 3; in this case the average daily weight increases are 42.55g/day and 47.59g/day respectively.

5 DIET

5.1 Introduction

Several studies have been made of the diet of Shags and Cormorants, often based on the analysis of the stomach contents of shot birds (Steven, 1933; Lumsden and Haddow, 1946; Duncan, 1968; Pearson, 1968; Mills, 1969a; Berry, 1976). In addition, studies of diet have also been based on the analysis of regurgitates, or of pellets (Van Dobben, 1952; Snow, 1960; Duncan, 1968; Mills, 1969b; Ainley *et al*, 1981).

Analysis of pellets has been used in a number of species of Cormorant, but their existence in the Shag seems to have been almost completely overlooked. Snow (1960) collected small numbers of Shag pellets, and looked at diet on the basis of the otoliths and other hard parts they contained. She states that the existence of Shag pellets is "a fact not previously mentioned in the literature of this species". This omission is curious in the light of those studies, listed above, based on pellets in a number of closely related species.

The advantages of pellets make them particularly useful in the case of a study such as the present one in which the examination of diet is carried out concurrently with the gathering of behavioral data. In this situation it is obviously undesirable to remove birds from the population, or to handle them in order to obtain regurgitates. There are, however, caveats which should be observed when basing a study of diet entirely on pellets: these are examined in the discussion.

5.2 Methods

5.2.1 Collection Of Samples

The analysis of diet was based on two types of sample: pellets, regurgitated by the adult birds, and stomach contents regurgitated by chicks.

Pellets were collected on a systematic basis during June and August 1985, and from January to August 1986. In both 1985 and 1986 pellets were also collected in October by Dr M P Harris. Collection was always in the morning, since pellets were rarely found later in the day, except on days when there was constant rainfall. It seems likely that pellets are produced largely through the night, or early in the day. Their production is rarely seen, and was recorded when it occurred during the time-budget watches. 15 pellets were seen being produced, and of these 14 were produced in the morning, the latest being produced at 1108 GMT. The other pellet was produced at 2108 GMT. There appeared to be two reasons for the disappearance of pellets later in the day: Shag pellets are very moist and dry out easily, after which the residue is quickly dispersed; in addition, gulls were observed to pick up and eat pellets on a number of occasions

Except during January and February, when collection of pellets occurred during a single trip, it was originally intended to collect at least 30 pellets for each month, with collection spread though the month. This target was not always met because, although pellets were very common in the breeding areas in the early part of the season, they became much less common once the chicks began to hatch. This was probably due to the birds spending less time roosting in the breeding areas once they had chicks.

Pellets were collected in sample jars, and were preserved in 96%

ethanol.

Regurgitates from chicks were collected opportunistically, usually when chicks were handled for the purposes of ringing or weighing. These were placed in plastic bags when collected, and were preserved by freezing.

5.2.2 Analysis Of Regurgitates

Regurgitates were weighed before freezing, and intact fish were measured. With only one exception, all of the fish regurgitated by chicks were sandeels. The number of fish represented in the samples by fragments was estimated by counting heads and tails. Whichever was the most numerous was taken as representing the number of fish contained in the sample. Lengths were estimated for fragments by reference to "standard" sandeels. These were fish which had been brought in by Puffins, and represented the four lengths typically brought in (75mm, 100mm, 130mm, and 170mm). It is assumed that these four lengths correspond to age classes.

5.2.3 Analysis Of Pellets

A sample of 15 pellets was randomly selected for analysis from the pellets collected within each month. A sample size of 15 was chosen because this represented the lowest sample size, since in June 1986 only 15 pellets had been found. The pellets were initially analysed by a method derived from that suggested by Murie and Lavigne (1985) for the analysis of the stomach contents of seals.

The pellets were first removed from the ethanol in which they had been stored, and were placed in water. It was necessary to soak them in water for several hours to soften them sufficiently for analysis. This was usually done overnight.

The pellets were then washed, one at a time, through 6 stacked sieves of decreasing mesh sizes. The meshes used measured 1.7mm, 1.0mm, 0.85mm, 0.71mm, 0.42mm, and 0.25mm. When all of the material left in the top sieve was too large to wash through the mesh, the sieve was removed and the contents of the second sieve were washed until all the material remaining in it was too large to pass through the mesh. This process was repeated for all of the sieves.

The contents of each sieve were then washed into a black photographic dish, and the otoliths were removed using a pipette. Otoliths were counted and identified as they were recovered from the dish.

This method suffered from two main problems: it was extremely time-consuming, each pellet taking at least 30 minutes to process; and it was laborious, requiring sustaining concentration over long periods of time.

It was thus replaced by a method adapted from one suggested by Harkonnen (1986). Pellets were first soaked for 24 hours in a solution make up of 10 parts water to 1 part of a strong solution of "Quadralene" glass-washing detergent. After soaking, the detergent solution was poured off, and the pellets were rinsed in two or more changes of fresh water. They were then soaked in a solution of sodium hydroxide made up by dissolving 10g of sodium hydroxide granules in 100ml of water.

After 12 hours, the mucous parts of the pellet had dissolved, leaving only the otoliths and other hard items, such as sand, stones and nest material. The sodium hydroxide solution was then poured off and replaced by fresh water, after which the residue was poured into a black photographic dish. The otoliths could then be removed and identified.

While the time necessary for counting the otoliths was the same as before, this process dramatically reduced the time needed to free the otoliths from the mucous parts of the pellet, since much larger samples of pellets could be processed at the same time.

5.3 Results

5.3.1 Regurgitates

In 1985, 19 regurgitates were collected, and in 1986, 38 regurgitates were collected. The mean weight of these regurgitates was 48.7g (sd 28.4) in 1985, and 44.0g (sd 34.0) in 1986. With only 2 exceptions, all regurgitates consisted entirely of sandeels (*Ammodytes sp*). In 1985, one regurgitate was made up almost entirely of a dragonet (*Callionymus lyra*), and in 1986 one regurgitate contained a fish which could not be identified, but which was recognisably not a sandeel.

5.3.2 Pellets

In each monthly sample, almost all of the otoliths extracted from the pellets were sandeel otoliths. These made up between 88.9% (October 1986) and 99.6% (August 1986) of the total number of otoliths extracted from each sample (see Table 5.1).

In addition, small numbers of otoliths of the following species were found: whiting (*Merlangius merlangus*), cod (*Gadus morhua*), spratt (*Sprattus sprattus*), herring (*Clupea harengus*), long rough dab (*Hippogolssoides platessoides*), dab (*Limanda limanda*), poor cod (*Trisopterus minutus*), Norway pout (*Trisopterus esmarkii*) and mackerel (*Scomber scombrus*). Crustacean remains were also found in a number of samples.

Table 5.1

Breakdown of the contents of Shag pellets by month. The figures given are the number of otoliths of each species extracted from a sample of 15 pellets from each month. Sandeel otoliths were the most common in each sample, and the percentage, by number, of sandeel otoliths for each month is also given.

Table 5.1

Month	Sandeel	Cod	Poor cod	Mackerel	Whiting	Norway Pout	Herring	Sprat	Unident-ified clupeoid	Flatfish	Unident-ified	Total otoliths	Sandeels %
July 85	898	17							2			917	97.9
Aug 85	894		2	2					1	6		905	98.8
Oct 85	2177	9			1		3	4		48		2242	97.1
Jan 86	2483	2		2	2		2	3		30		2542	98.4
Feb 86	2168	5					3	5	13	12	6	2212	98.0
Mar 86	2974	14	2			2		5		28	6	3031	98.1
Apr 86	4159							9	3	17		4188	99.3
May 86	2316	3			3					18		2343	98.8
June 86	681								2	1	6	690	98.7
July 86	678	4			2				6	6		696	97.4
Aug 86	1034	3										1038	99.6
Oct 86	683	68							8	9		768	88.9
Mar 87	1902	3	2		2				12	13		1934	98.3

5.4 Discussion

5.4.1 Methodology

Pellets have several advantages over analysis of stomach contents or regurgitates which render them extremely useful in the study of diet. Their collection involves minimal disruption to the birds, since there is no necessity either to remove birds from the population, or to handle them. In addition, pellets may easily be gathered in large numbers, and samples may be taken from the same area on a number of separate occasions.

Against these advantages, however, must be weighed the cautions of studies which have identified limitations in the use of pellets to examine diet. Hartley (1948) considered a number of methods of investigating diet in birds. He noted that for some species, such as the larger owls, the comparison of pellets with stomach contents showed a very close correlation between the two, whereas in other species pellets held no trace of important prey species. He concluded that pellets alone should never be used in food studies, save when preliminary studies have established their quantitative and qualitative adequacy.

Ainly *et al* (1981) cite two studies, plus their own data, to suggest that pellets are equivalent to stomach samples in cormorants. However, a recent study which examines the contents of pellets produced by Shags from the Isle of May under controlled conditions (Johnstone *et al*, 1990) suggests that this is not true for all species of *Phalacrocoracidae*.

Johnstone *et al* fed fish of known size and species to 2 adult male and 2 adult female Shags in captivity, then analysed the pellets which were produced. They found that the otoliths recovered from pellets were significantly smaller than those taken from fresh fish, and estimated that any otolith under 3mm long would be digested completely. The prey families which would thus be overlooked in a study based entirely on pellets are *Zoacidae*, *Pholidae*, *Labriidae*, *Callionymidae* and *Gasterosteidae*. They suggested that the larger *Ammodytidae*, *Clupaidae* and *Gadidae* would be detectable from the analysis of pellets.

They concluded that a great deal of work needs to be done before general diet studies can be carried out based on the analysis of pellets; the current state of knowledge does not permit meaningful quantitative statements to be made about diet composition solely on the basis of pellets.

5.4.2 Results

The present study was based largely on the analysis of pellets, supplemented by the examination of regurgitates. The overwhelming majority of the otoliths recovered derived from *Ammodytidae*, a result which is not surprising in the light of the work by Johnstone *et al.* It is important to note, however, that otoliths were recovered from a number of other species, and that crustacean remains were also found. Whilst remaining ever mindful of the limitations of pellets as a basis for studies of diet, it is still possible to make qualitative statements about diet composition even if quantitative statements can only be regarded as speculative at best.

The results of this study suggest that sandeels are an important prey species for Shags on the Isle of May. This conclusion does not depend entirely on the analysis of pellet contents: of 57 regurgitates which were collected, only 2 contained fish other than sandeels.

The importance of sandeels as a prey species appears to be true throughout the year, including those months which sandeels are believed to spend overwintering buried in the sand (Winslade, 1974). Winslade suggests that sandeels enter an overwintering stage in August, and remain buried until April, emerging only to spawn in the December-January period. The presence of sand in those samples taken in October of each year, January to May 1986 and March 1987, suggests that at these times the birds are taking sandeels from the bottom, and that during the summer months the birds are taking free-swimming fish.

Other studies of Shag diet have also tended to find sandeels an important constituent of diet. Pearson (1966) working on the Farnes found sandeels accounted for 81% of the diet in terms of number of items. Lumsden and Haddow (1946) in the Clyde sea area found sandeels making up 54% of the diet, but this varied from none at all in Shags fishing over a rocky sea floor to 72% in Shags fishing over a sandy or muddy floor. Steven (1933) found 33% sandeels in Shag stomachs from Cornwall, and Snow (1960) on Lundy found large numbers of small sandeel otoliths in pellets. Only Mills (1969), working on Shags fishing in the sea loch Loch Ewe, found other species to be more important than sandeel. Large numbers of Sandeel otoliths were found, but only in a few stomachs. The most important species in this study, in terms of the number of stomachs in which their otoliths occurred, were gadoids and herring.

In conclusion, the results of this study justify the statement that sandeels are an important prey species for Shags on the Isle of May, as they are in other locations. This statement is supported not solely by the composition of the otoliths recovered from pellets, but also by the composition of the regurgitates which were taken. At the same time, Shags clearly take a number of other species; the exact composition of the diet of Shags on the Isle of May is a subject for future studies. It is to be hoped that the present study has shown at least the variety of prey species taken by Shags from the Isle of May.

6 THE TIME BUDGET OF THE SHAG

6.1 Introduction

Time budgets may be thought of as encompassing simultaneously all of the costs and benefits of an animal's activity. The efficiency of an animal in allocating its time to the various activities it must perform ultimately influences its fitness in terms of the number of surviving offspring it produces.

Time budget data may be collected very easily in the field, and can provide a basis for answering questions relating to activity changes through the breeding season, allocation of resources between the sexes, and differences in breeding success between different animals. Additionally, time budget data may be used as a basis for the estimation of energy budgets (Orians, 1961; Schartz and Zimmerman, 1971; Custer and Pitelka, 1972; Utter and LeFebvre, 1973; Ashkenazie and Safriel, 1979; Ettinger and King, 1980; Weathers and Nagy, 1984; Bernstein and Maxson, 1985).

The present study was concerned with estimating a time budget for the Shag. On open sites, such as those typical of the Isle of May, the Shag is an ideal bird for observation because it may easily be caught and marked, and it habituates well to the presence of observers. The data presented here relate to the activity of the Shag at the nest site.

6.2 Methods

Observations were made throughout the breeding season, beginning during the late pre-lay period, and ending during the late-brood period, when the chicks became highly mobile, and the parents spent decreasing amounts of time in the breeding areas.

Observation sessions typically lasted 2 or 3 hours, and were staggered in such a way that complete dawn to dusk cover was obtained over 3 or 2 days respectively. Observations were made using a checksheet, on which the activities of the focal birds were recorded every 30 seconds following a tone from an electronic metronome.

Four nests was found to be the maximum number which could accurately be followed at one time. Accordingly, during each dawn to dusk cover observations were made of a group of four nests. Different groups of nests were used in each successive series of observations.

Although some of the time spent off the nest was spent in the study area, this was frequently in parts of the study area removed from the nest sites, such as the sea rocks. It was not found to be possible to make accurate observations of activity on the nest, and to keep track of birds away from the nest. Consequently, time absent from the nest does not represent time spent away from the breeding area.

During the incubation and brooding stages, the birds spent most of the time they were present at the nest sitting, due to the necessity to incubate eggs or brood chicks. Thus, most behaviours such as preening or sleeping, were performed simultaneously with incubating or brooding. A bird was scored as "rest" if it was sitting on the nest and doing nothing else. Thus, although "rest" is not synonymous with incubating or brooding, changes in this category reflect changes in the amount of time spent incubating or brooding.

The breeding cycle was divided into three stages, for the purpose of analysis: the incubation stage, the brood stage, and the post-brood stage. The incubation stage commenced with the date of the first egg, and ended with the hatching of the first chick. The brood stage was defined as a period of 21 days from first hatch. The post-brood stage was defined as commencing 22 days after the first hatch.

Observations were made of a total of 13 nests. Of these, 2 failed to lay eggs, 1 was very late, and 2 lost their chicks during the brood stage. Of the remaining 8 nests, data were collected on each breeding stage from 7 of them, and from only 2 stages for the remaining nest. The results presented below are derived from the 7 nests from which data were collected during each stage.

6.3 Results

6.3.1 Attendance

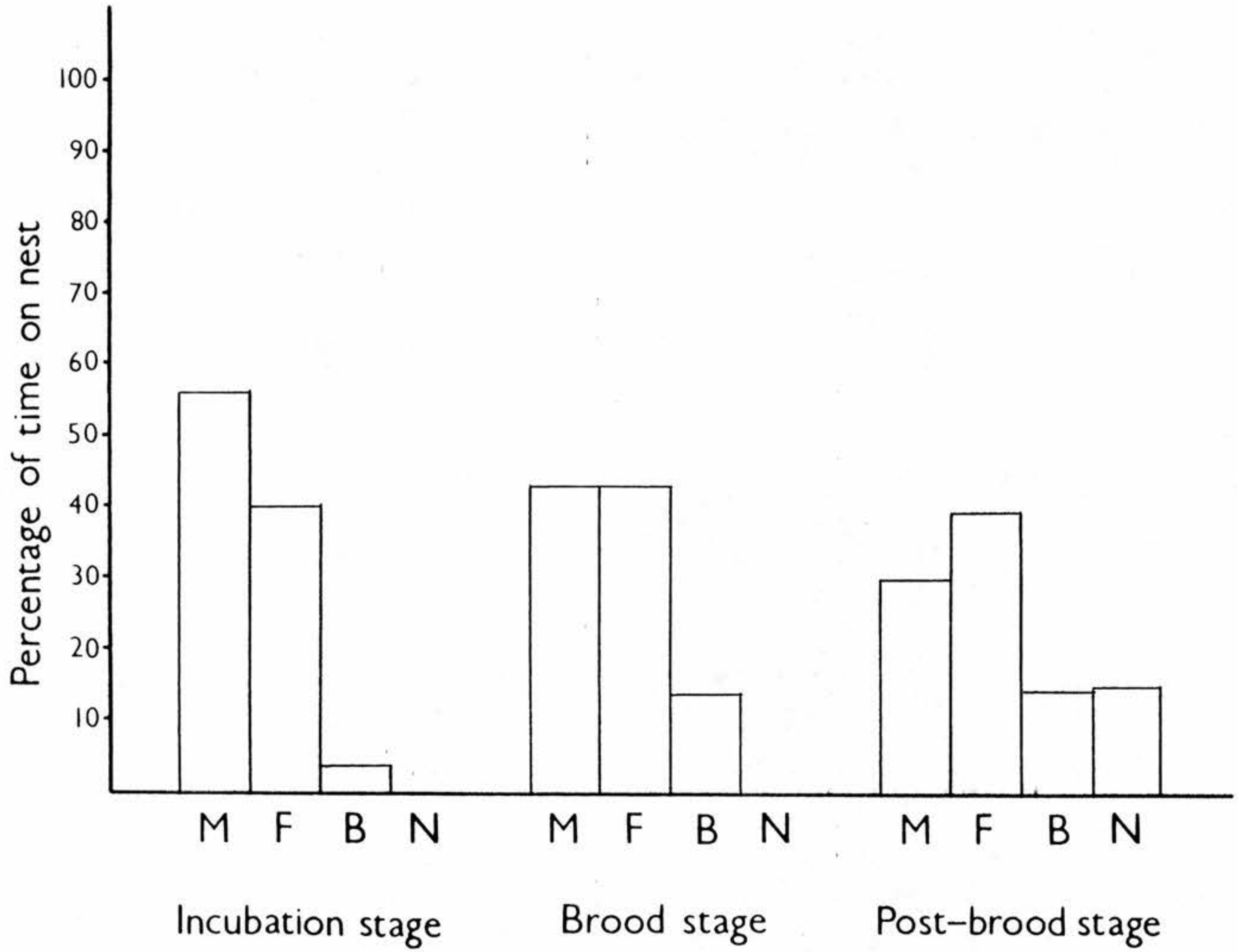
During the incubation and brood stages, the nest must be attended constantly by at least one adult, if it is to produce chicks. If the nest is left unattended, even for a few minutes, it is rapidly destroyed by neighbouring birds which remove the nest material for their own nests, with the loss of the contents of the unattended nest. An unattended nest is also at risk from predation by gulls, which will take eggs or young chicks. During the post-brood period, attendance is not so predictable. Although the adults will defend the site when present, they spend very little time on nest maintenance, and on more exposed sites the nest can disappear completely before the chicks are fully fledged.

From the incubation stage to the post-brood stage, the male spends progressively less time alone on the nest ($F = 13.32$, $p < 0.01$), and the adults spend progressively more time together on the nest ($F = 3.68$, $p < 0.05$). The attendance of the female alone on the nest was not significantly different between stages. During the post-brood stage only, the nest was left unattended for 15% of the time (Fig 6.1).

Figure 6.1

The amount of time spent on the nest by the male alone (M), the female alone (F), both adults together (B), and neither adult (N). Incubation stage is the period from the date of the first egg to the date of the first hatch; brood stage is a period of 21 days from the date of first hatch; post-brood stage commences 22 days after first hatch. Data are derived from 7 nests from which data were collected during each stage.

Figure 6.1


Percentage of time on nest
100
90
80
70
60
50
40
30
20
10
M
F
B
N
Incubation stage
M
F
B
N
Brood stage
M
F
B
N
Post–brood stage

6.3.2 Time Budgets

24 categories of activity were recorded, out of which 5 accounted for between 95.7 and 98.8% of the time budget. These categories were: time absent from the nest, preen self, rest, stand, preen chick, and sleep. The remaining 17 categories made up a maximum of 4.3% of the time budget, and were not analysed individually.

The data were analysed by analysis of variance to answer two questions: does the time budget differ between the sexes? and how does the time budget change as the breeding season progressed? There were no sex differences for any of the six major categories. All of the categories except "time absent" and "preen chick" showed differences between breeding stages, and "sleep" showed an interaction between sex and breeding stage (Fig 6.2). These differences were investigated further using the Newman-Keuls test. The results of this analysis are summarised in Table 6.1.

6.4 Discussion

From the incubation stage to the post-brood stage, males spent progressively less time alone on the nest, and the amount of time both birds spent together on the nest progressively increased. The amount of time spent alone on the nest by the females remained constant throughout, and the total amount of time spent on the nest by the male was not significantly different between stages.

These results do not suggest that the birds have to spend a greatly increased amount of time fishing as the chicks grow older. This suggests that supplies of fish are readily available around the Isle of May. That this is so is also indicated by the continuing increase in the numbers

Figure 6.2

Variation through the breeding season of the 6 main categories of behaviour in males (o---o) and females (x---x). I is incubation stage (first egg - first hatch); B is brood stage (21 days beginning from first hatch); P is post brood stage (22 days from first hatch onwards). All categories except "time absent" and "preen chick" show significant differences between breeding stages.

Figure 6.2

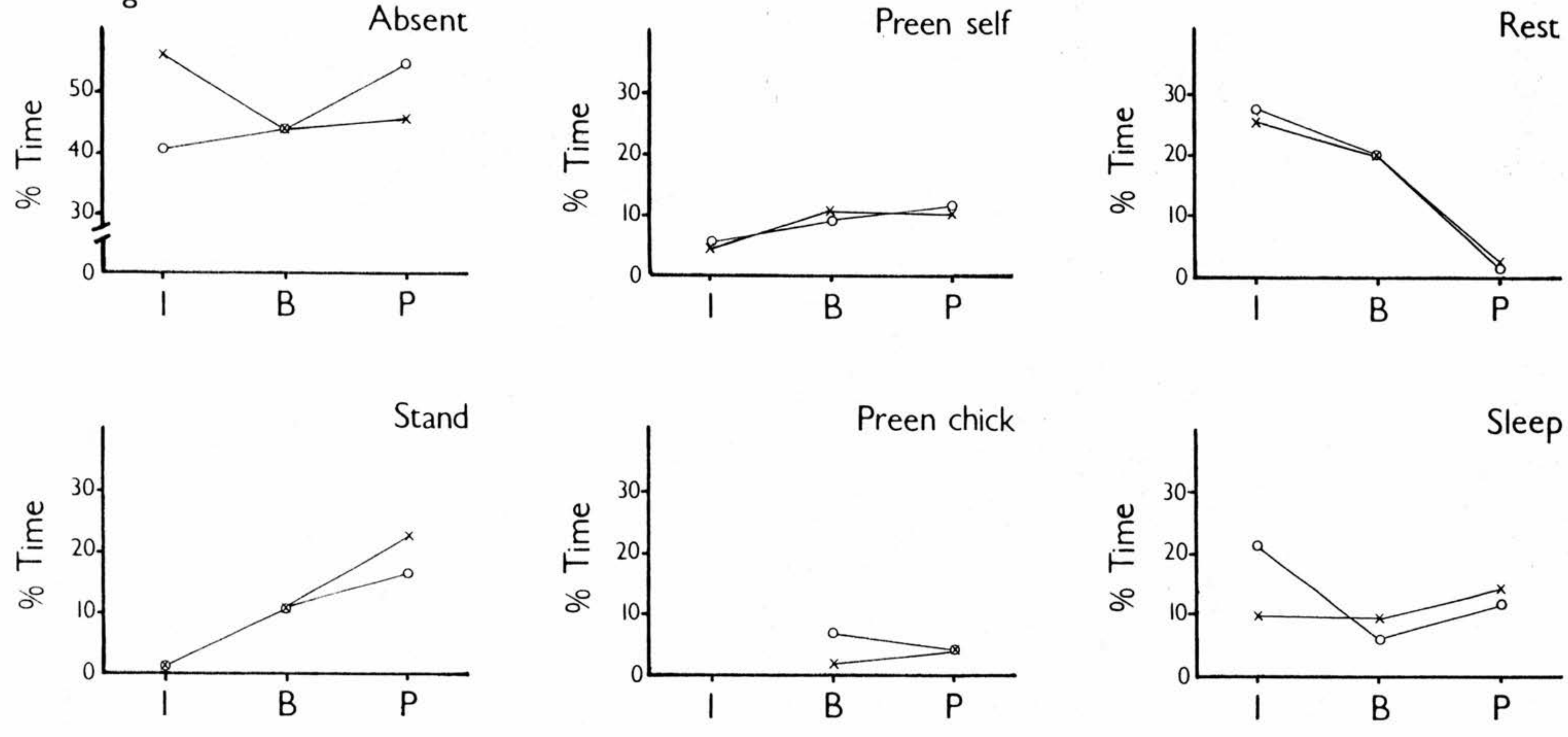

Absent
Preen self
Rest
Stand
Preen chick
Sleep
% Time
0
30
40
50
10
20
I
B
P

Table 6.1

Summary of the Newman-Keuls analysis of the differences between breeding stages in the 6 main categories of behaviour. The analysis is for both birds together, for males only, and for females only.

Where there is a significant difference between breeding stages, this is shown on the table, and the level of probability is given in parentheses.

Two categories, time absent and preen chick, showed no significant differences between breeding stages, and thus do not appear on the table.

Table 6.1

Effect due to breeding stage

	Brood	Post-brood
Incubation	Preen self (p<0.05) Rest (p<0.05) Stand (p<0.05) Sleep (p<0.05)	Preen self (p<0.05) Rest (p<0.01) Stand (p<0.01)
Brood		Rest (p<0.01) Stand (p<0.05)

Within sex effect - male

	Brood	Post-brood
Incubation	Stand (p<0.05) Sleep (p<0.01)	Rest (p<0.01) Stand (p<0.01) Sleep (p<0.05)
Brood		Rest (p<0.01)

Within sex effect - female

	Brood	Post-brood
Incubation	Preen self (p<0.05)	Preen self (p<0.05) Rest (p<0.01) Stand (p<0.01)
Brood		Rest (p<0.01)

of Shags, and other species, on the Isle of May (Aebischer, 1985; Harris, 1985).

There were no sex differences in any of the major time budget categories, suggesting that there are no great differences between males and females in the responsibilities of raising chicks.

Other than "time absent", all of the categories showed differences between breeding stages. The most marked changes were in the categories "rest" and "stand". From the incubation stage to the post-brood stage, the amount of time devoted to "rest" decreased, and the amount devoted to "stand" increased. This is due to the diminishing dependence of the offspring on brooding as the breeding season progresses.

Little is known about the activities of the birds away from the nest. This is a problem of far greater complexity than that of making observations at the nest, due to the difficulty of keeping track of individuals when they are flying, or on the sea. Certainly, sightings of colour-marked birds from the focal area roosting at the north end of the island suggest that it is not sufficient to regard all time spent away from the focal area as being taken up by flying to and from feeding areas and by fishing.

Time budgets have been used as a basis for the estimation of energy budgets, using suitable conversion factors for the energetic costs of such behaviour (Orians, 1961; Schartz and Zimmerman, 1971; Custer and Pitelka, 1972; Utter and LeFebvre, 1973; Ashkenazie and Safriel, 1979; Ettinger and King, 1980; Weathers and Nagy, 1980; Williams and Nagy, 1984; Bernstein and Maxson, 1985). There is some doubt about the accuracy of this methodology. Three of the studies cited above (Utter and LeFebvre, 1973; Weathers and Nagy, 1980; Williams and Nagy, 1984) used both the time budget method and the doubly labelled water method to estimate energy expenditure in free ranging birds. Weathers and Nagy found substantial differences between estimates derived from the two methods, the time budget method yielding an estimate almost 40% lower than that obtained by the double labelled water method. Utter and LeFebvre found a maximum difference of 19.1% between estimates derived from the two methods, and attributed this to deficiencies in sampling activities when estimating the time budget. The closest agreement was found by Williams and Nagy, who compared estimates derived from the doubly labelled water method with time-energy budget models from the literature, and found differences between the two methods to be less than 6%. Speakman and Racey (in press) have suggested that the doubly labelled water technique gives estimates of energy expenditure accurate to within 5%.

The greatest obstacle in studies of this type is the lack of adequate data on the energetic costs of different activities. This is illustrated by Bernstein and Maxson's (1985) study of the reproductive energetics of the Blue-eyed Shag, in which many of the conversion factors used to derive the energy budget from the time budget are taken from studies of passerines. It seems likely that this could result in substantial errors when attempting to estimate an energy budget for a large seabird, especially one that feeds underwater.

The current state of knowledge with respect to large seabirds is not sufficient to allow the estimation of energy budgets with an acceptable degree of accuracy. In particular, there is a serious lack of data relating to activity at sea. Coupled with this is an absence of data on the energetic costs of fishing and swimming underwater, both of which are crucial activities for seabirds. These gaps need to be filled before it becomes possible to derive meaningful time and energy budgets for seabirds.

7 DISCUSSION

7.1 Monitoring

The results of comparing counts of nests with accurate data on the exact number of nests present confirmed that early June was the best time to make a count. This result is particularly interesting in view of the fact that 1986 was a late season for the Shag on the Isle of May, the first eggs being recorded during the first week in May.

The result would not have been so clear had this study been undertaken in 1985. This year was characterised by very poor weather conditions during the early part of the season, which delayed the time when the birds could commence breeding. Thereafter, it appeared to resemble very closely the type of "crash" year examined by Aebischer (1985, 1986). Only about one third of the nests in the study area produced chicks compared with the number that was expected based on data from previous seasons (j Graves, unpublished data).

There appeared to be a high rate of mate change throughout the breeding season, accompanied by a high turnover of nests, as sites were abandoned and reoccupied. However, very few systematic observations were made, and the data does not allow a detailed treatment of this behaviour.

Under these conditions, it is unlikely that a count at any time during the breeding season would have given an accurate index of the number of breeding pairs, since it seems likely that throughout the season, the number of nests exceeded greatly the number of pairs which eventually produced chicks. Again, observations made were insufficient to allow for a detailed analysis.

The lesson to be learned from this is that it is not sufficient simply to make a census count at the required time. There should also be an assessment of the ultimate breeding success wherever possible, particularly if unusual or extreme weather conditions have prevailed early in the season.

No-one has, as yet, made a detailed on-the-spot study of failure to breed in the Shag, which appears to occur periodically (Aebischer, 1985, 1986). Aebischer's work sheds some light on the phenomenon, and clearly shows that seasons characterised by unusually low breeding rates are not the result of massive adult mortality. However, the actual dynamics of a "crash" year remain unclear. Nonetheless, it seems certain that a normal "one off" census count will not give a valid estimate of the breeding population under these conditions.

7.2 Feeding Biology And Time Budget

Shags on the Isle of May do not appear to be stressed for food. Harris (1985) has reported findings which suggest that conditions around the Isle of May are favourable for seabirds, and the work described here does not contradict this result.

Three results support the idea that conditions for Shags on the Isle of May are currently very good. Both males and females spent large amounts of time at the nest site, and once the chicks had hatched they did not appear to increase the amount of time they spent away from the nest, which suggests that there was no difficulty in finding sufficient food for the chicks.

Analysis of the growth rates of the chicks did not show any difference between broods of one, two or three chicks. Pearson (1968) considered the growth rates of chicks to be a sensitive indicator of the ability of the parents to supply them with food. It may be concluded that around the Isle of May there is sufficient food available to allow the successful rearing of broods of three chicks without any detriment to their growth or final weight. In addition, comparison of the growth rates obtained from this study with those presented by Snow (1960) and Pearson (1968) shows no difference in daily weight increase between these studies.

The final piece of evidence derives from the work of Aebischer (1985). The Shag population on the Isle of May has been growing for much of this century, and is continuing to grow (Aebischer, 1985). This again suggests that food supplies around the Isle of May are very good, sufficient not only to support the existing population, but to accommodate an increase in the numbers of birds.

To complete the picture of the activity pattern of the Shag, data need to be collected covering the time spent by the birds away from the nest. This currently remains an area in which there is very little definite information, though there are some indications emerging of what the birds do away from the nest.

Work currently in progress involving the radio-tracking of Shags (Wanless, pers. comm.) indicates that the roost site on North Ness, at the north end of the island, is used by birds which are feeding. A male and a female, which were given radios during the egg stage, were found to fly from North Ness to feeding sites off Fife Ness and St Monans, and to return to North Ness after feeding. They were observed to fly several times between the fishing grounds and North Ness, before returning to the nest.

Interestingly, a sample of seven birds (4 males and 3 females) which were given radios once the chicks had hatched, were not observed to do this, and on feeding trips went straight from the nest site to the feeding grounds, and straight back to the nest after feeding.

This work is still currently at a preliminary stage, and a great deal remains to be done. However, it does suggest that there are differences in feeding patterns between the egg stage and the brooding stages which are not revealed simply by considering observations made at the nest-site. Thus, while the time spent away from the nest by breeding birds is not significantly different during the brooding stages compared with the incubation stage, it appears that the birds are spending more of the time they are away from the nest actually feeding, once they have chicks.

The timing of feeding appeared to be dependent on the time of day, and to be unrelated to the tidal cycle. This is in accord with Snow's (1963) observations. The importance of time of day in the feeding of Shags is probably related to the behaviour of sandeels, which follow a diurnal cycle of activity, dependent on light. Kuhlman and Karst (1967) studied free-swimming sandeels in the Western Baltic, and noted that sandeels spent the night buried in the sand on a sandbank. They emerged at sunrise, congregating in schools of increasing size, before heading out in large numbers to feeding grounds in deep water, about 1000m from the shore. Here they remained until about midday, when they returned to the coastal strip, and wandered about the sand bottom in large numbers until evening, beginning to search for a resting place about an hour before sunset.

Kuhlman and Karst (1967) give no information relating to the behaviour of sandeels during the winter months, since their work was conducted during the summer. There is some evidence (Winslade, 1974) to suggest that sandeels overwinter buried in the sand. The presence of large quantities of sand in pellets collected during the winter months suggests that at these times the birds are, in fact, feeding on the bottom. N Upton (pers comm) has observed Shags fishing on the seabed by swimming along with the bill in the sand, a method of fishing not previously recorded for the Shag, which is generally regarded as taking fish from mid-water (eg Lack, 1945).

A feeding study of the Shag during the winter months remains to be carried out. It will be interesting to determine whether or not Shags continue to follow a diurnal pattern of feeding, or whether their feeding habits change in response to the change in the behaviour of the sandeel.

7.3 Energy Budgets

There is very little information relevant to energy use by large seabirds. Some work has been done on the costs of flight in gulls (Baudinette and Schmidt-Nielson, 1974; Tucker, 1969, 1972), and on the cost of swimming in ducks (Prange and Schmidt-Nielson, 1970), and Furness (1978) has examined energy flow through seabird communities, but there are no studies comparable to those which have been done on passerines (eg Utter and LeFebvre, 1973; Walsberg and King, 1978; Ashkenazie and Safriel, 1979; Hails and Bryant, 1979; Ettinger and King, 1980; Weathers and Nagy, 1980; Williams and Nagy, 1984).

The Shag is an ideal bird for this type of work, since it may easily be captured and recaptured, which is essential in doubly-labelled water studies, and it is large enough to carry monitoring equipment, such as the radio transmitters used to measure heart rate (eg Owen, 1969; Morhardt and Morhardt, 1971).

The absence of any direct measurements of the energetic costs of activity for seabirds means that no matter how detailed or complete a time budget estimate is produced, any energy budget estimate which is subsequently derived from it will be of questionable value.

The study of the energy requirements of seabirds is a topic of increasing importance as the growth of fishing industries brings closer a conflict of interests between Man and birds (Crawford and Shelton, 1978; Furness, 1978; Abrams, 1985).

APPENDIX A.

Worksheets Used in the Hide

a ATTENDANCE WORKSHEET: This was simply a handwritten list of nest numbers, against which attendance was recorded every 15 minutes.

Attendance was recorded as follows:

- if the male or female was present on the nest, this was recorded using the appropriate symbols.
- if the nest held chicks, the presence of a chick was recorded using the letter c.
- if an intruder was present on the nest, or if the nest site was not permanently occupied, the colour rings of the bird were recorded following the convention a/b - c where
  a is top colour
  b is bottom colour
  c is leg on which rings were held
  Colours were identified by initial letter, or first two letters; black was identified by N (niger).
- if a site was occupied by an unknown bird (ie not colour ringed) this was recorded by the letter P (present).

b TIME BUDGET WORKSHEET: This was a pre-printed form with nest number at the top of each column. Each "nest" column was then subdivided into a column for the male and a column for the female. Four nests were studied during each session.

Activity was recorded for each bird at one minute intervals, signalled by a metronome. Activity was recorded using mnemonics. The carat symbol (^) indicated that the bird was not on the nest site. S before any activity indicated that the bird was standing to perform the activity.

Mnemonics used to record activity were:

PS	preen self
PM	preen mate
R	rest (sitting)
S	stand
W	walk
Q	quiver nest material
C	courtship (dart-gape, throw-back, bow, throat click)
PB	pairbond maintenance (upgape, bow, bill, throat click)
COP	copulate
CF	chick feed
CP	chick preen
BPt	bill point
TG	threat gape
ST	stand threat
MO	mobile threat
SL	sleep

31.7.85 2.00pm – 4:00

	2:00	:15	:30	:45	3:00	:15	:30	:45	4:00
1	—	—	—	—	—	—	—	—	—
2	—	—	—	2/Y-R	—	—	—	—	—
3	—	—	Y/R-L	〃	〃	〃	〃	—	Y/R-2
3′	Y/R-L ABOVE —	〃 —	—	—	—	—	—	—	—
4	—	—	—	—	—	—	—	—	—
7	—	—	W/Y-L	—	—	—	W/Y-2	♂, ♀	〃
7′	♂	—	—	Y/Y-2	〃	〃	—	✓	—
9	Y/Gy-L	—	Y/Gy-L	〃	〃	—	—	—	Y/Gy-L,
9′	—	—	—	—	—	—	—	—	—
11	—	?♂, ♀	—	—	—	—	—	—	—
11a	♂, ♀ cs	〃	♂, c	〃	〃	〃	〃	〃	〃
bd 11a	♀ c.	〃	〃	〃	〃	♂, ♀, c	〃	〃	〃
13	✓ STOR	〃	✓	✓	—	—	—	—	—
13a	W/Bl-R	〃	W/B-R	—	—	♂ 2nd yr	〃	—	—
14	—	—	—	—	—	—	—	—	—
14a	—	—	—	—	—	—	—	—	—
15	—	G/W-R	—	✓	—	G/W-R	〃	〃	—
16	♀/cs	♂, ♀, cs	〃	〃	〃	〃	♂, cs	♂, ♀, cs	♂, cs
16a	14♂, c	〃	〃	〃	〃	〃	〃	〃	〃
17	—	—	—	—	G/W-R	single G-2	〃	〃	SINGLE-G Br/B-2
17′	—	W/Y-R	—	—	—	—	—	—	—
18	—	—	—	—	—	—	—	—	—
18′	—	—	—	—	—	—	—	—	—
19	—	—	R/W-L, W/Y-L	〃	〃	R/W-2	〃	〃	〃
20	—	—	B/Br-R	—	—	—	—	—	—
				11 ♂, ♀ on 11/14	〃	〃	〃	—	—

TERVAL :30s

DATE: 1/7/86

TIME: 6·00pm–8·00pm

#1

WIND: M
DRN: SW
VIS: G
TIDE: L

	1		2		3		3'			1		2		3		3'	
	♂	♀	♂	♀	♂	♀	♂	♀		♂	♀	♂	♀	♂	♀	♂	♀
		SPS	SCP	S	SPS	↓SPS	R				SPS	SPC	SPS	SPS	S	S	
		SPS	S	S	SPS	SPS	S				SPS	SPC	SPS	SPS	SSL	S	
		SPS	S	S	SPS	SPS	S				SPS	SPC	SPS	SPS	SSL	S	
		SPS	S	S	SPS	SPS	S				SPS	SPC	SPS	SPS	SSL	S	
		S	S	S	SPS	SPS	S				SPS	SPC	SPS	SPS	SSL	S	
		SPS	SCP	SQ	SPS	SPS	S				SPS	SPC	SPS	SPS	SSL	S	
		SPS	S	S	SPS	SPS	S				SPS	SPC	SPS	SPS	SSL	S	
		SPS	SPC	S	SPS	SPS	SPS				SWS	SPC	S	SPS	SSL	S	
		SPS	SPC	S	SPS	SPS	S				SPS	SPC	SPS	SPS	SSL	S	
		SPS	SPC	S	SPS	↑SPS	S				SPS	SPC	SPS	SPS	SSL	S	
		SPS	SPC	↓SSL	SPS	SPS	S				SPS	SPC	↓SPS	SPS	SSL	S	
		SPS	SPC	SSL	SPS	SPS	S				S	SPC	SPS	SPS	SPS	S	
		SPS	SPC	SSL	SPS	SPS	S				SPS	SPC	SPS	SPS	SPS	SPS	
		SPS	SPC	SSL	SPS	SPS	S				SPS	SPC	SPS	SPS	SPS	SPS	
		SPS	SPC	SSL	SPS	S	SPS				SPS	SPC	SPS	SPS	SPS	SPS	
		SPS	SPC	SSL	SPS	SPS	S				SPS	SPC	SPS	SPS	SPS	SPS	
		SPS	SPC	SSL	SPS	S	S				SPS	SPC	SPS	SPS	SPS	S	
		SPS	SPC	SSL	SPS	SSL	S				SPS	SPC	SPS	SPS	SPS	SPS	
		SPS	SPC	SSL	SPS	SSL	SPS				SPS	SPC	SPS	SPS	SPS	SPS	
		SPS	SPC	↑SSL	SPS	SSL	S				SPS	SPC	↑SPS	SPS	SPS	SPS	
		SPS	SPC	S	SPS	S	S				SPS	SPC	SPS	SPS	↓SPS	SPS	
		SPS	S	SPS	SPS	SSL	S				SPS	SPC	SPS	SPS	SPS	SPS	
		SPS	SPC	SPS	SPS	SSL	S				SWS	SPC	SPS	SPS	SPS	S	
		SPS	SPC	SPS	SPS	SSL	S				S	SPC	SPS	SPS	SPS	SPS	
		SPS	SPC	SPS	SPS	SSL	S				SPS	SPC	SPS	SPS	SPS	S	
		SPS	SPC	SPS	SPS	SSL	S				S	SPC	S	SPS	SPS	SQ	
		SPS	SPS	SPS	SPS	SSL	S				S	SPC	S	SPS	SPS	ST	
		SPS	SPC	SPS	SPS	SSL	S		2♀ on 4		S	SPC	S	SPS	SPS	S	
		SPS	SPC	SPS	SPS	SSL	S				R	SPS		SPS	SPS	SQ	
		SPS	SPC	SPS	SPS	SSL	S				R	SPS		SPS	↑SPS	SQ	

APPENDIX B.

Growth data.

Chicks were weighed from 12 broods of 1, 7 broods of 2 and 5 broods of 3. Weights are given in grammes.

Numbering convention is nest number followed by chick number, thus 4#1 is chick number 1 from nest 4; for broods of one, only the nest number is given.

BROODS OF 1

	3	4#1	5	19#2	25	27#2	28a
1.7	70	450	310	130	-	430	110
4.7	130	540	460	230	-	650	190
9.7	300	720	690	390	60	880	330
14.7	500	1000	950	650	170	1050	620
19.7	810	1200	1100	900	400	1350	1150
24.7	1000	1300	1300	1050	600	1300	1050
30.7	1350	1450	1500	-	-	-	-
31.7	-	-	-	1300	1000	1450	1300
5.8	1700	1650	1450	1500	1250	1550	1750
10.8	1750	1550	-	1500	1500	1500	1650

BROODS OF 2

	1#1	1#2	2#1	2#2	7#1	7#2	12#1	12#2	13#1
1.7	60	40	320	340	260	140	420	450	-
4.7	160	110	490	510	480	230	570	600	-
5.7	-	-	-	-	-	-	-	-	-
9.7	330	220	710	790	580	400	780	890	-
14.7	560	470	1000	1050	800	600	1050	1100	70
19.7	730	720	1300	1300	900	800	1200	1350	230
24.7	950	850	1450	1500	1100	900	1300	1400	450
30.7	1250	1300	1650	1750	1450	1200	-	-	-
31.7	-	-	-	-	-	-	-	1600	880
5.8	1550	1500	1800	-	1650	1500	-	1350	1300
10.8	1450	1600	1650	-	1700	1450	-	1350	1450

	13#2	16#1	16#2	22#1	22#3	23#1	23#2	24#1	24#3
1.7	-	-	-	240	140	360	240	-	-
4.7	-	50	-	360	160	510	470	-	-
5.7	-	-	-	-	-	-	-	-	-
9.7	-	170	60	570	310	770	740	740	690
14.7	40	360	160	850	550	1000	1050	1000	950
19.7	140	640	340	1050	800	1350	1400	1250	1300
24.7	280	1000	620	1250	1000	1450	1550	1350	1500
30.7	-	-	-	-	-	-	-	-	-
31.7	630	1300	1100	1500	1300	1750	1800	1700	1700
5.8	1050	1600	1250	1600	1650	1900	1900	1850	2050
10.8	1250	1650	DEAD	1500	1750	-	1900	1750	1950

BROODS OF 2

	26#1	26#2	29#1	29#2	30#1	30#2
1.7	110	60	220	120	50	40
4.7	190	130	-	240	-	-
5.7	-	-	360	-	120	100
9.7	350	270	570	410	240	230
14.7	640	550	900	670	530	490
19.7	1000	900	1150	1000	850	900
24.7	1100	1050	1450	1300	1100	1100
30.7	-	-	-	-	-	-
31.7	1500	1350	1700	1400	1350	1450
5.8	1850	1750	2000	1650	1700	1800
10.8	1900	1850	1900	1600	1750	1950

BROODS OF 3

	11#1	11#2	11#3	17#1	17#2	17#3	28#1	28#2	28#3
1.7	420	500	330	550	590	490	280	200	130
4.7	530	600	450	690	740	690	440	340	230
5.7	-	-	-	-	-	-	-	-	-
9.7	770	900	670	900	970	950	700	490	340
14.7	1050	1100	950	1150	1300	1100	950	700	590
19.7	1300	1300	1200	1350	1400	1400	1300	1000	800
24.7	1350	1450	1450	1450	1450	1400	1400	1050	1000
30.7	-	-	-	-	-	-	-	-	-
31.7	1450	1550	1850	1500	1550	-	1650	1400	1300
5.8	1500	1650	1850	1550	-	-	1900	1550	1550
10.8	-	-	-	-	-	-	1850	1600	1550

	28b#1	28b#2	28b#3	31#1	31#2	31#3
1.7	110	100	40	280	210	180
4.7	210	190	80	-	-	-
5.7	-	-	-	520	360	390
9.7	410	360	200	710	610	430
14.7	670	610	390	950	850	700
19.7	1050	950	650	1350	1150	1000
24.7	1150	1100	850	1450	1460	1050
30.7	-	-	-	-	-	-
31.7	1350	1400	1200	1650	1650	1350
5.8	1550	1650	1350	1850	1900	1600
10.8	1550	-	1500	1850	1800	1500

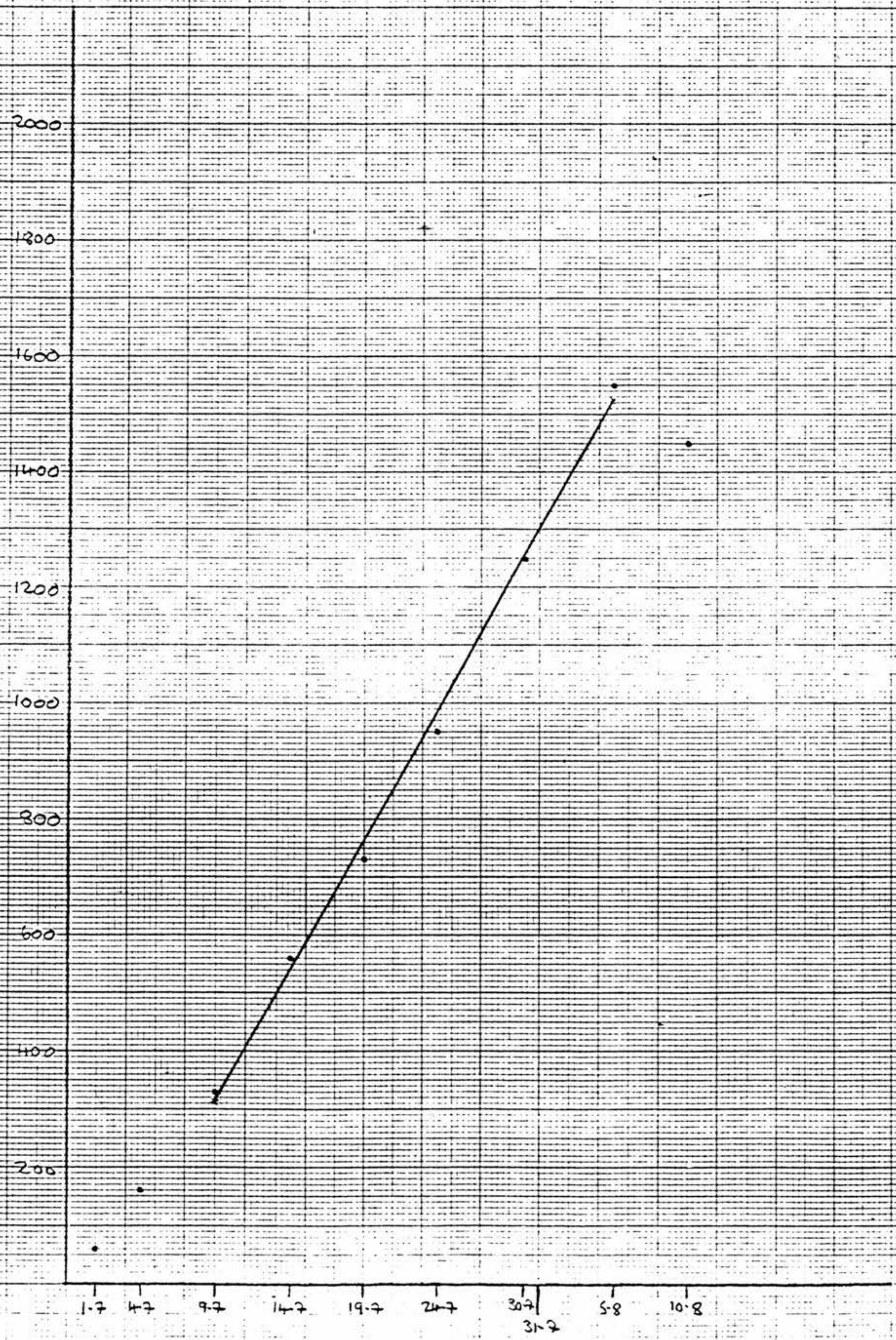
APPENDIX C.

Growth curves.

These are the individual growth curves for the chicks used in the weighing study.

Numbering convention is nest number followed by chick number, thus 4#1 is chick number 1 from nest 4; for broods of one, only the nest number is given.

1 #1



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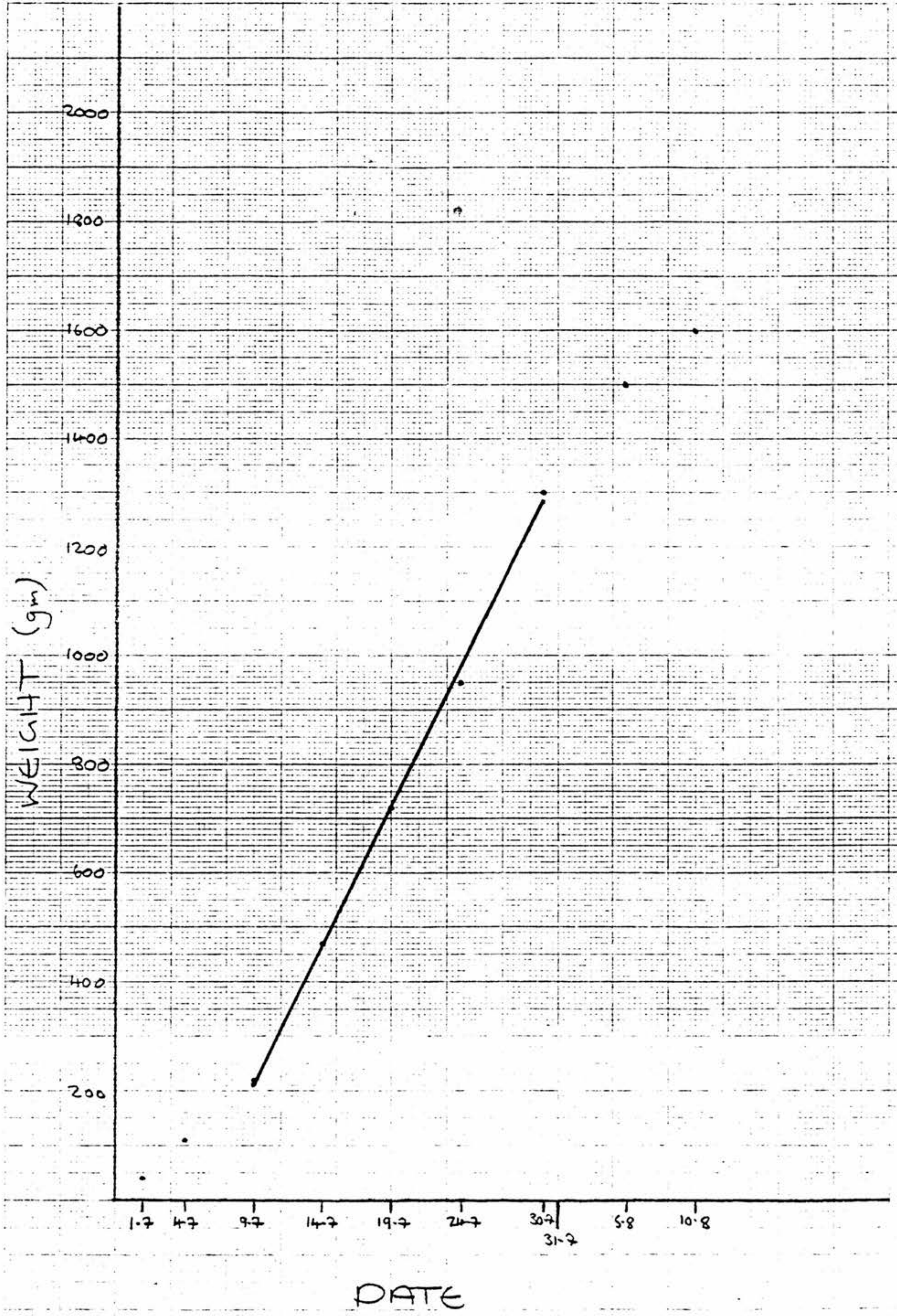

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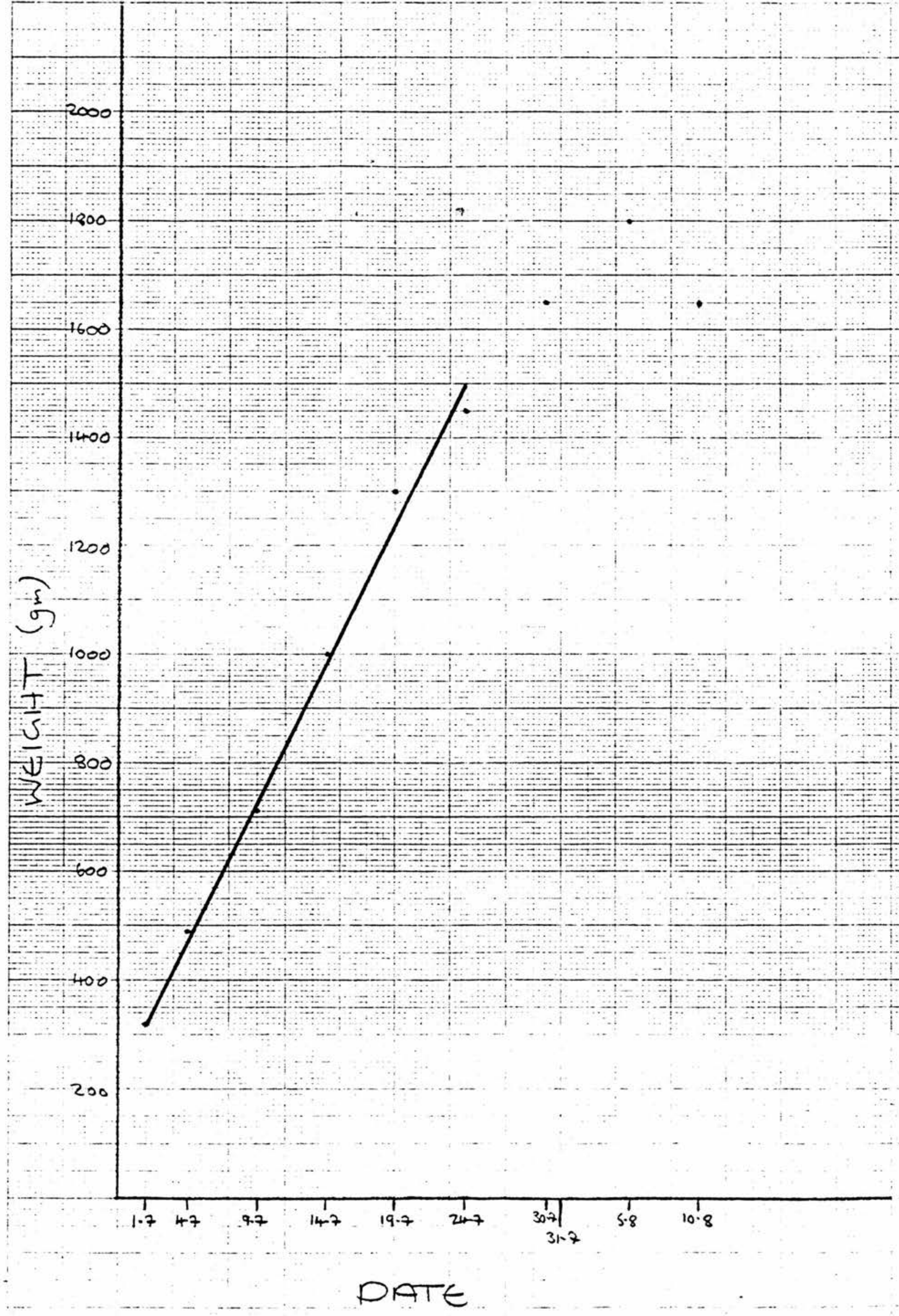
DATE

2#1



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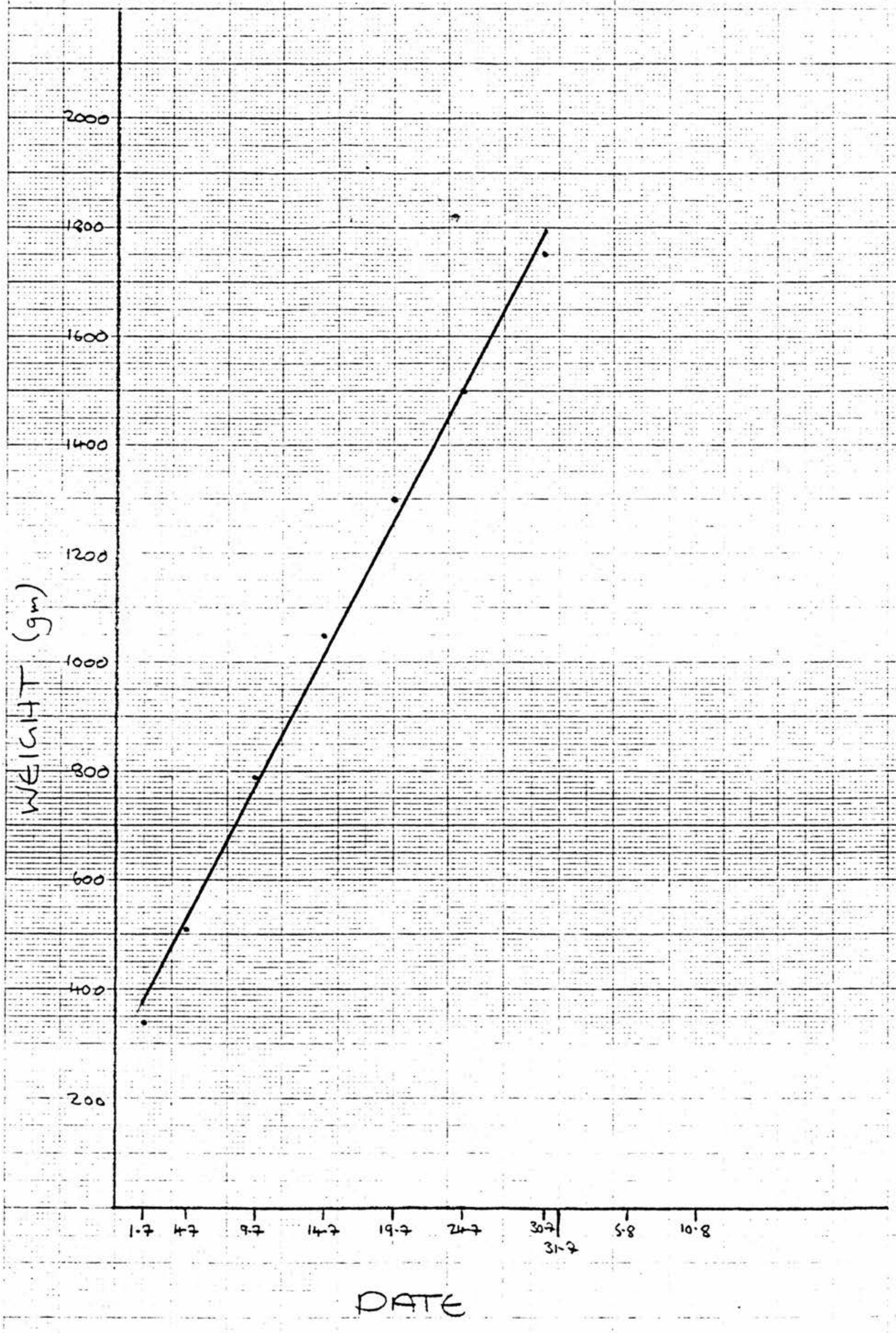
DATE

2#2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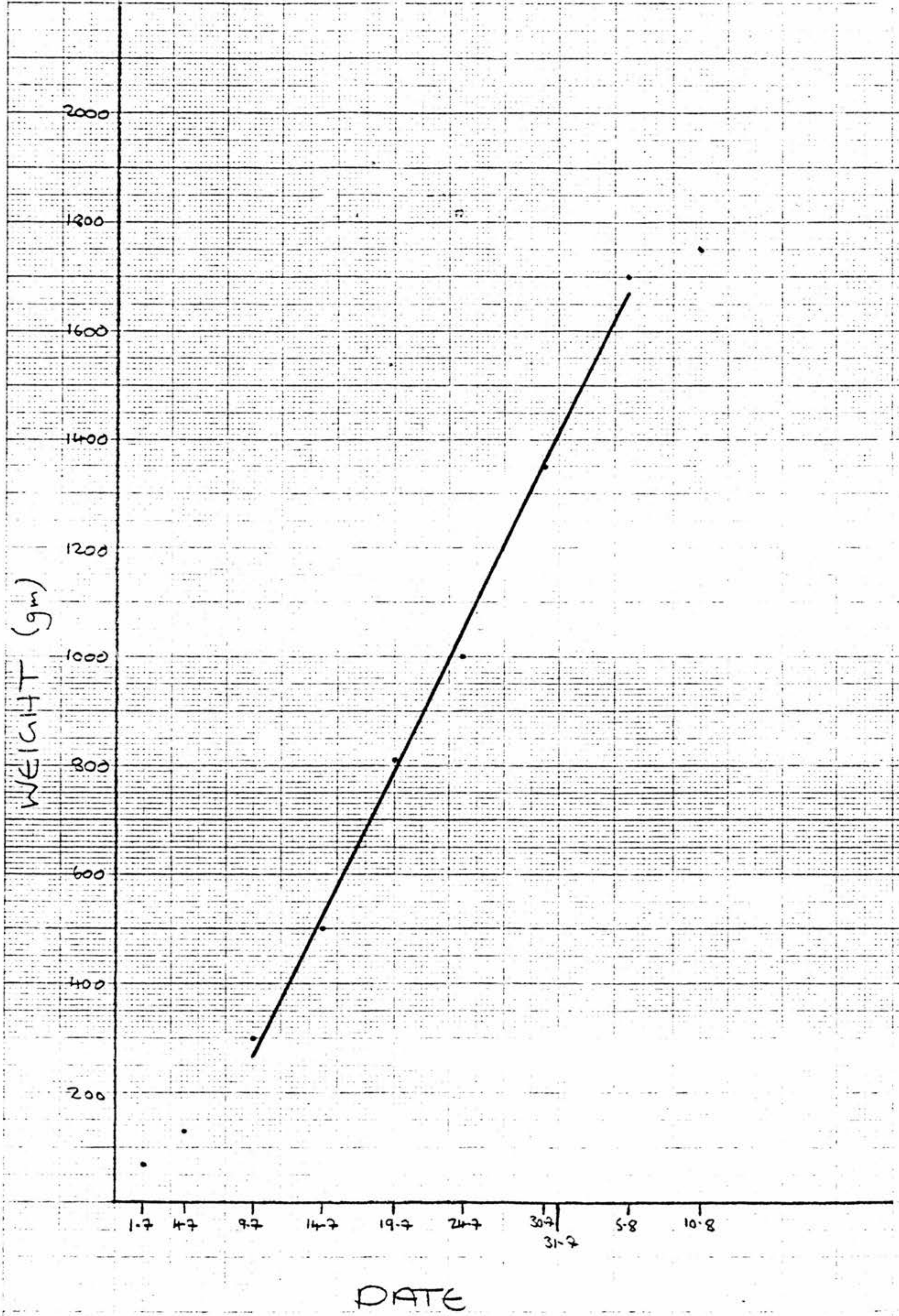
DATE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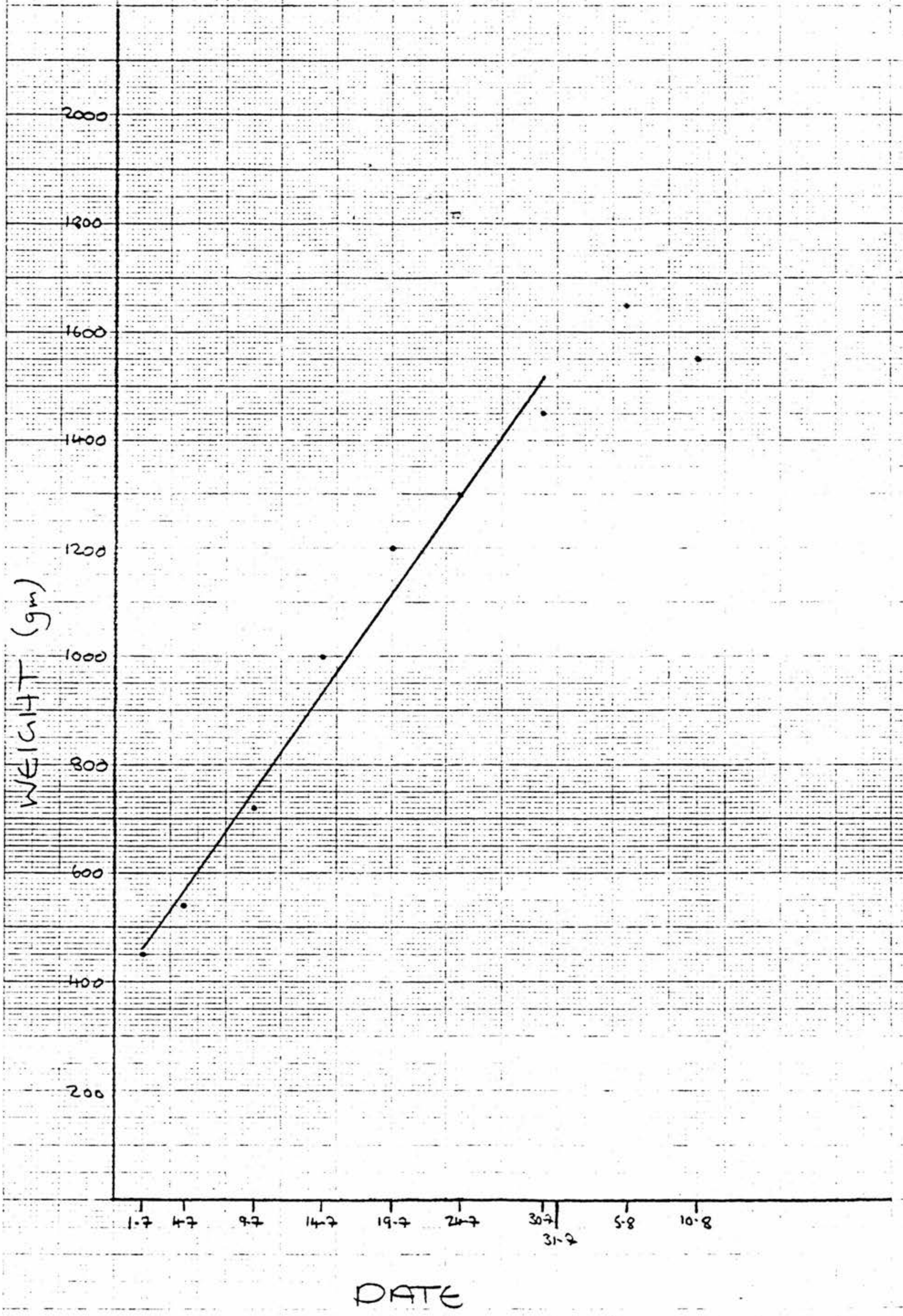
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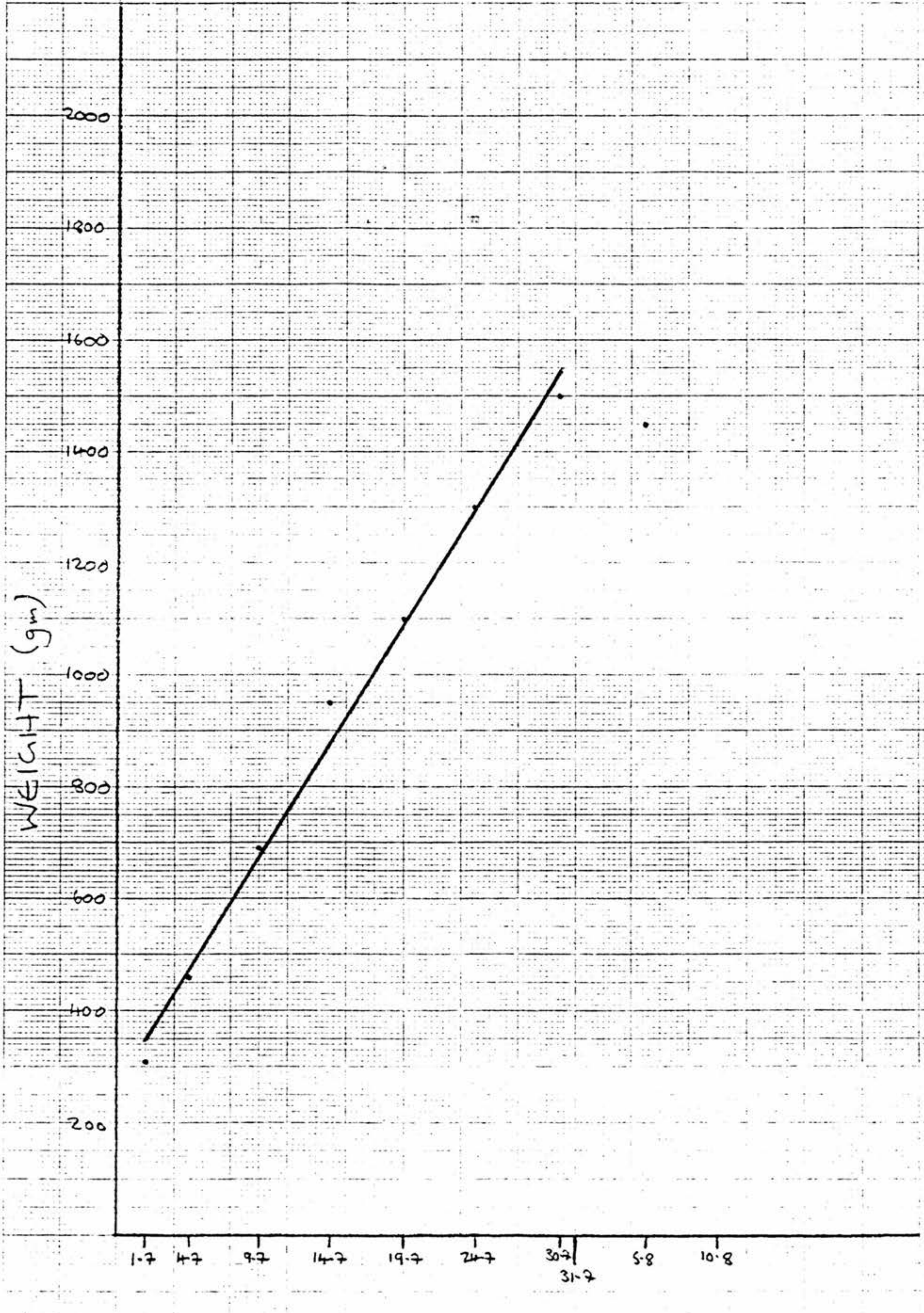
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WEIGHT (gm)
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DATE

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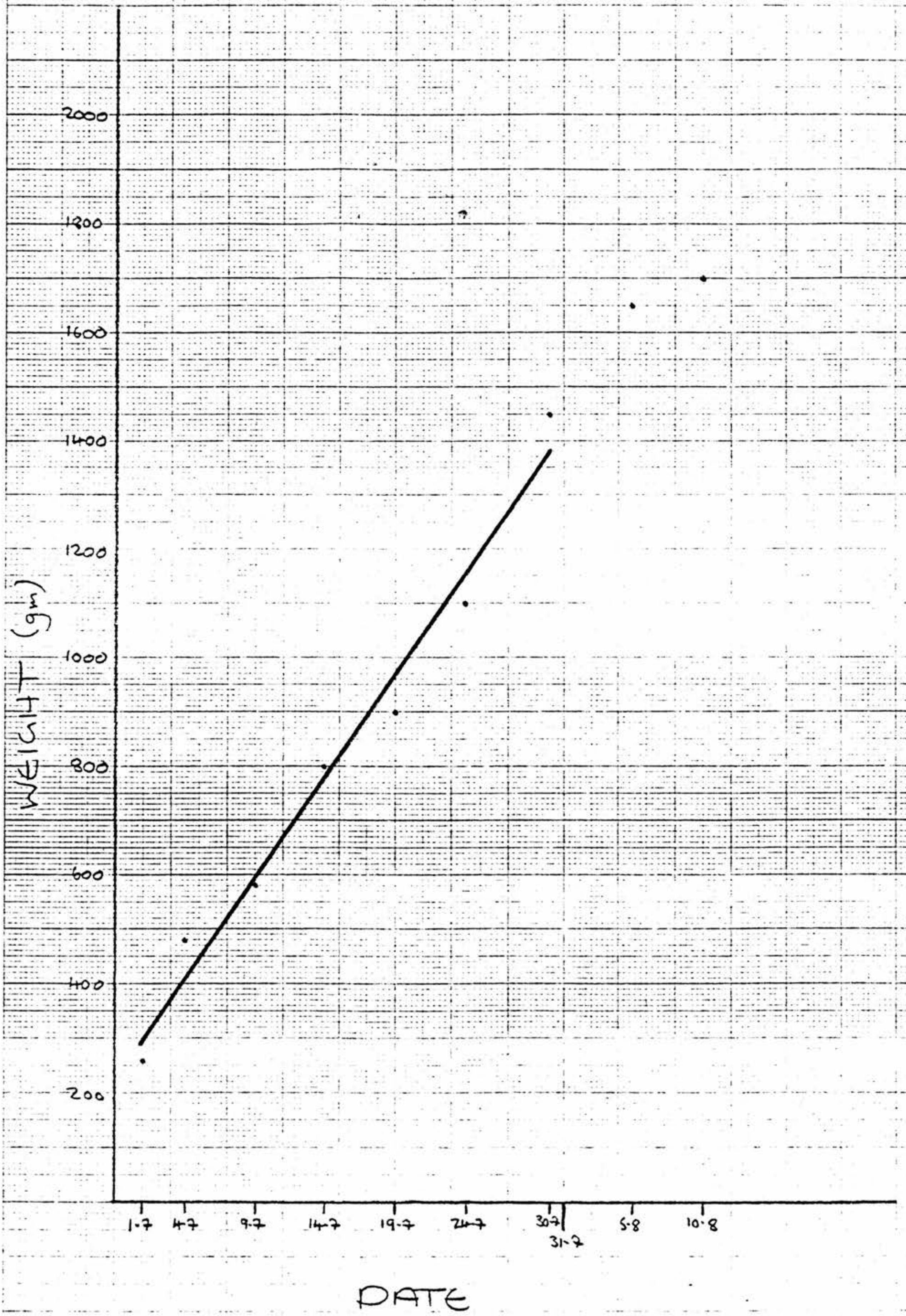
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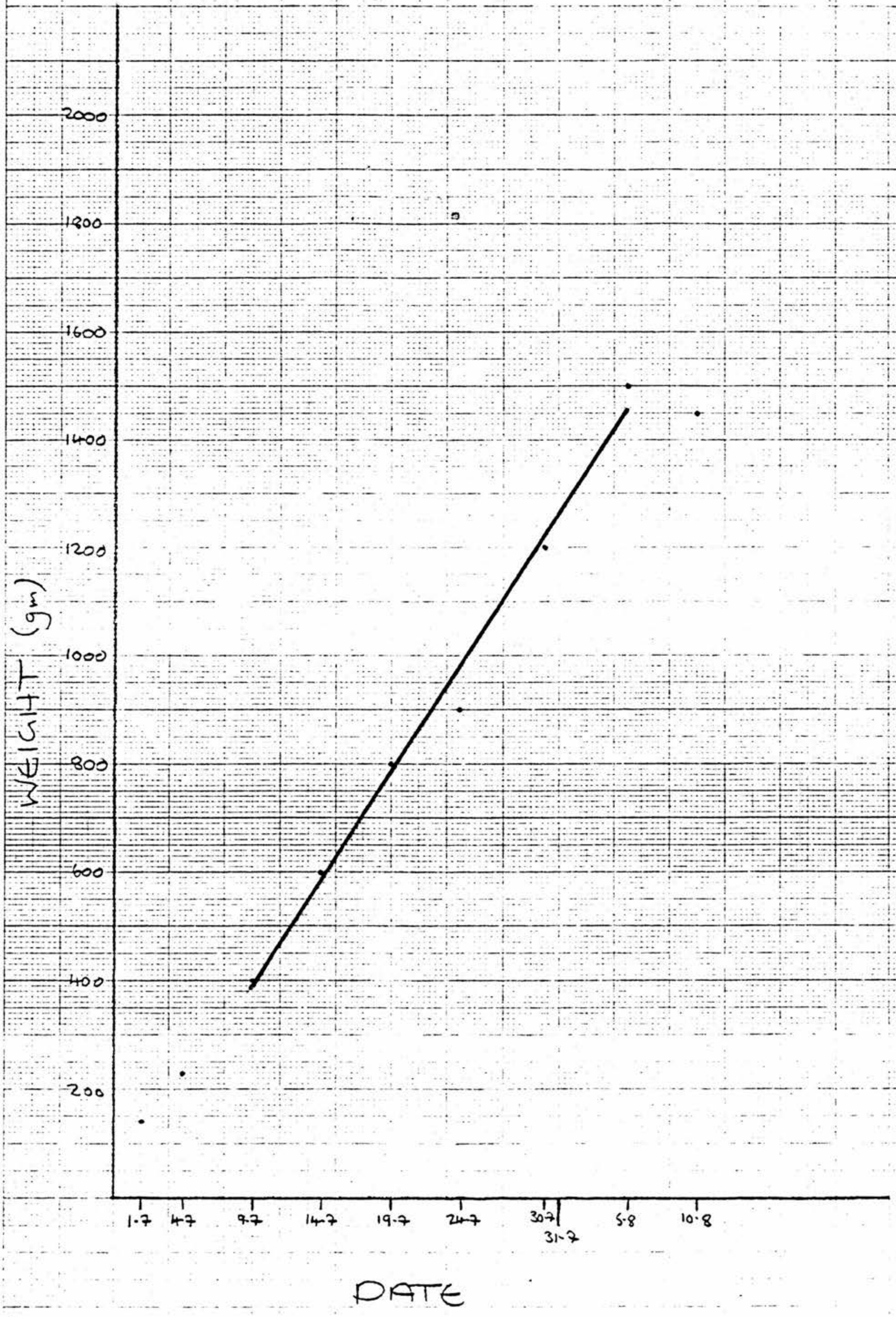
DATE

7#2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WEIGHT (gm)
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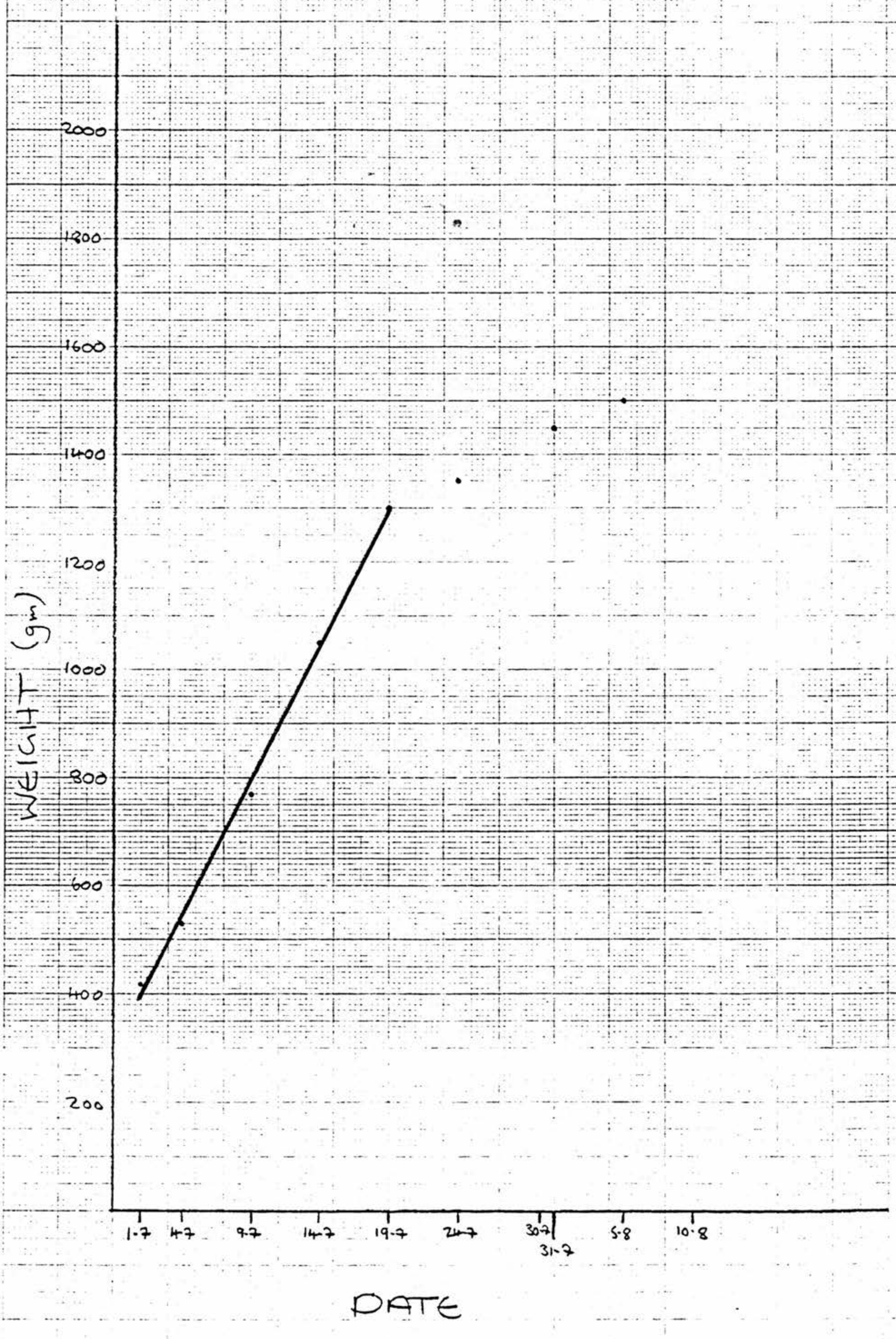
DATE

11#1



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DATE

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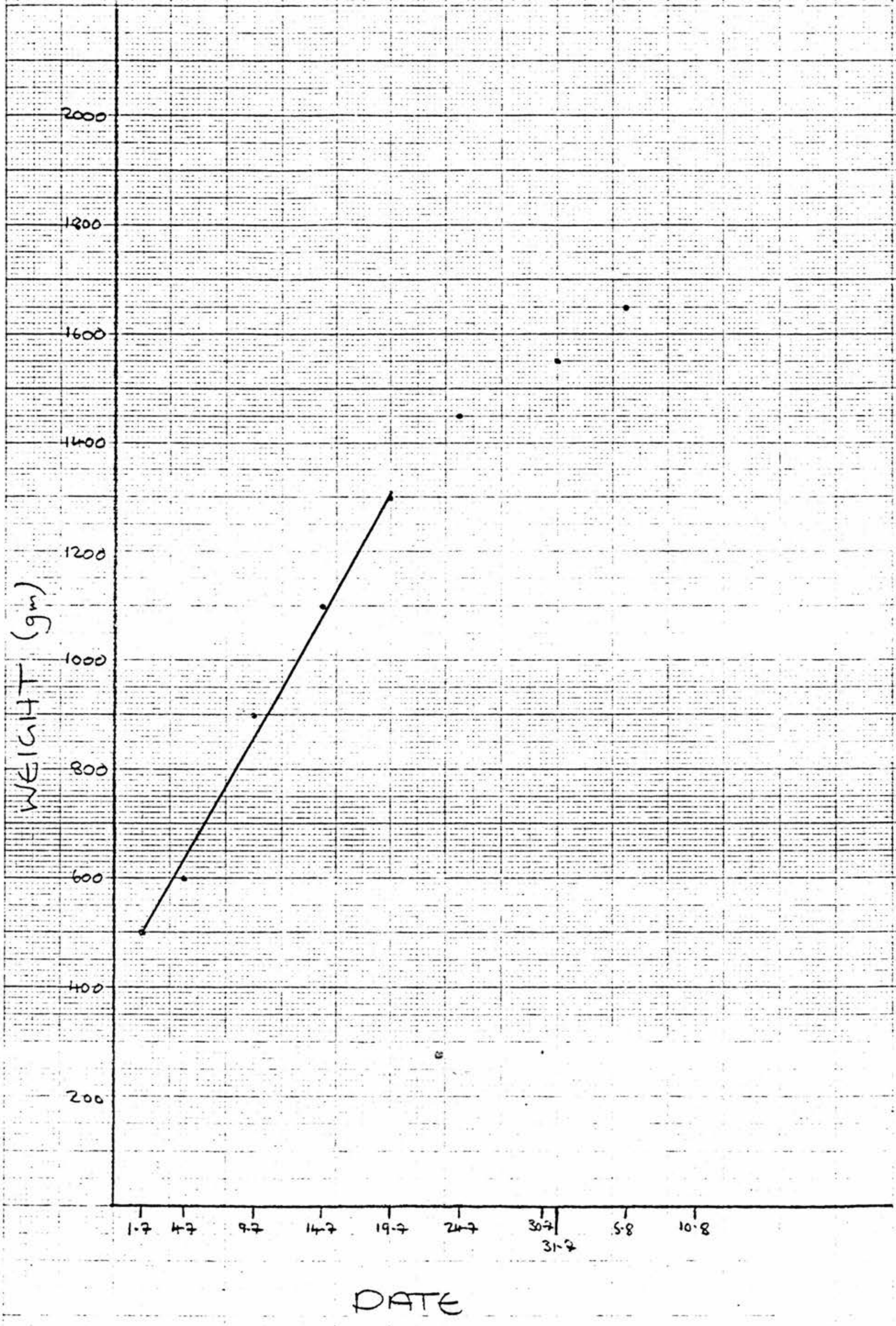

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DATE

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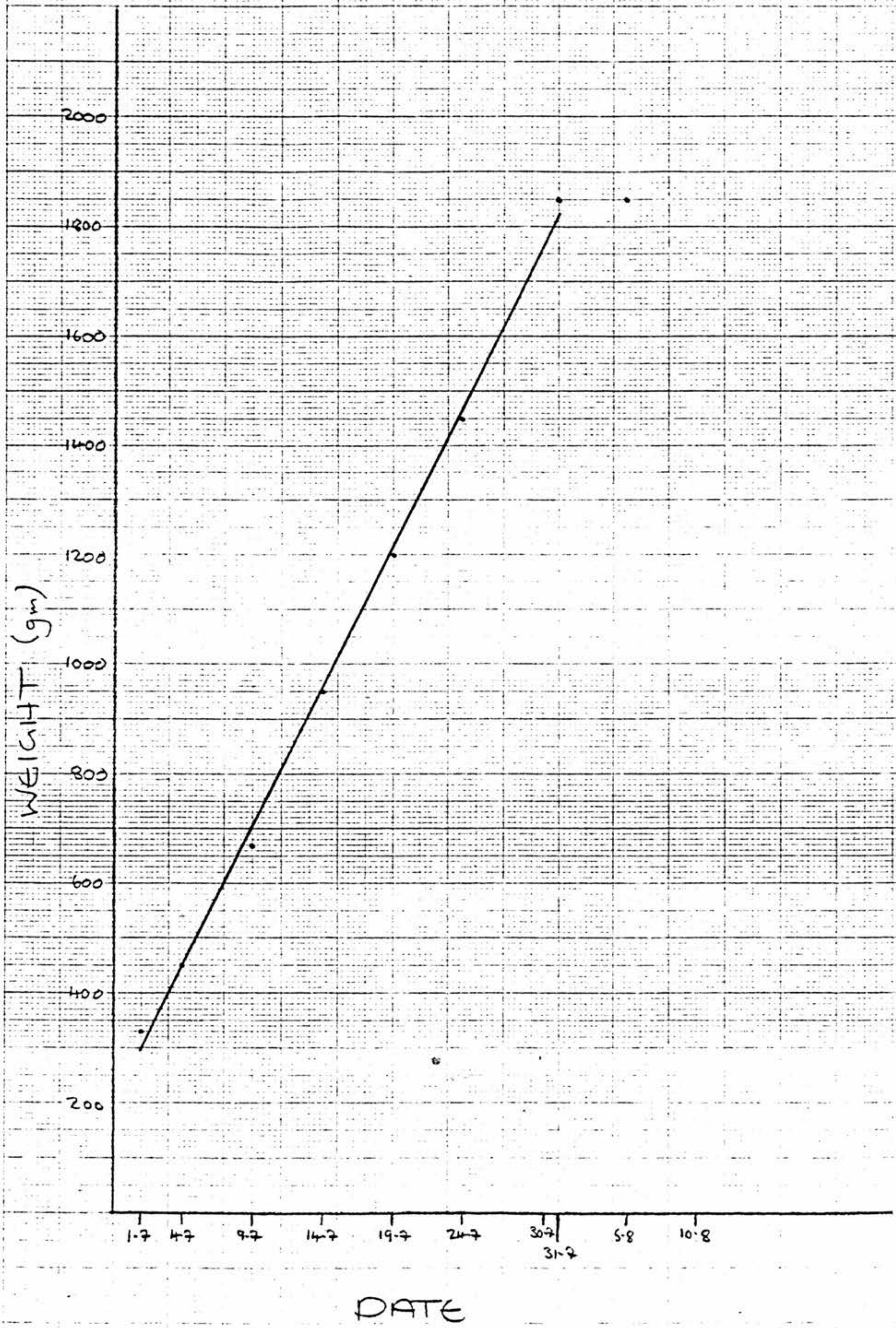
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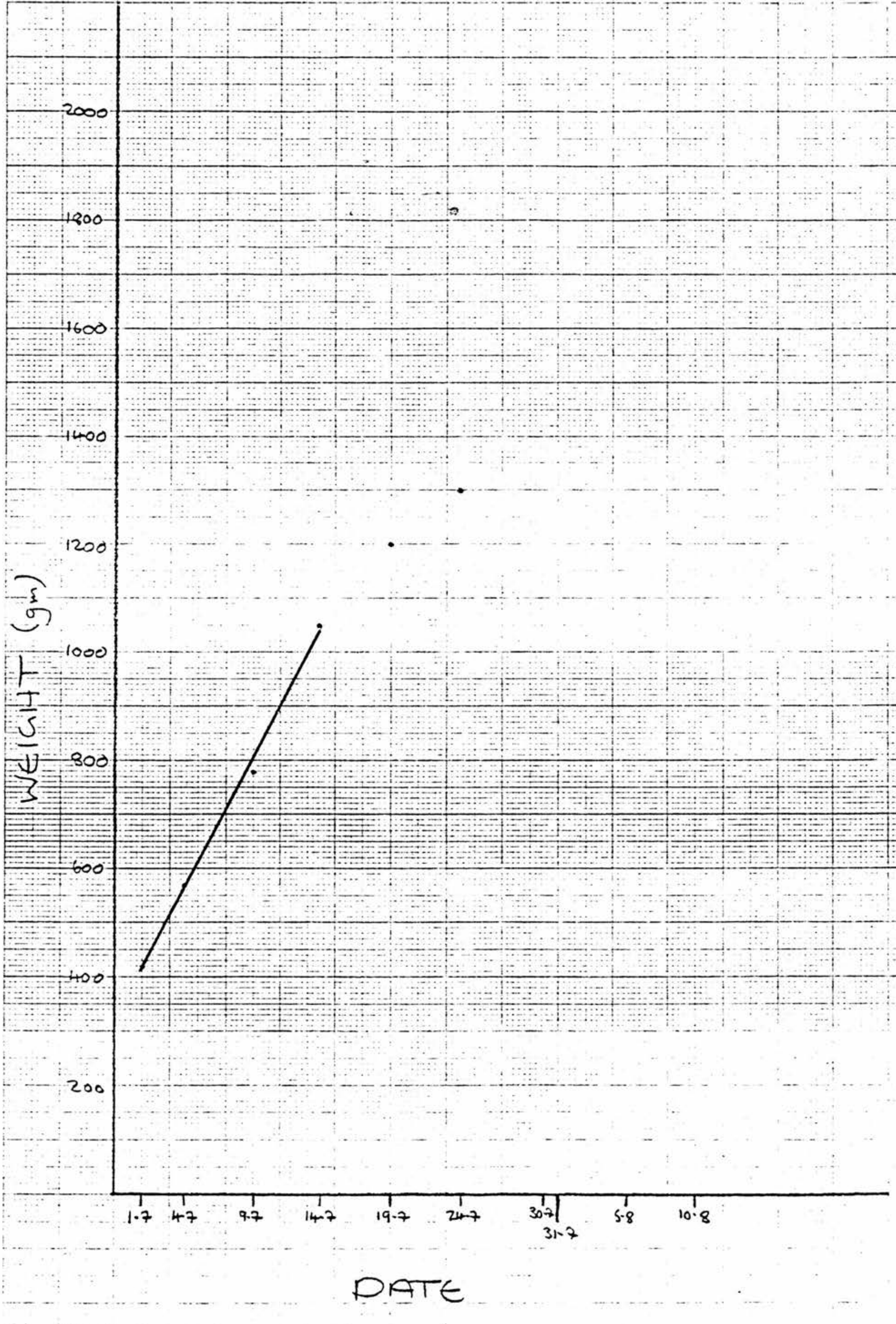
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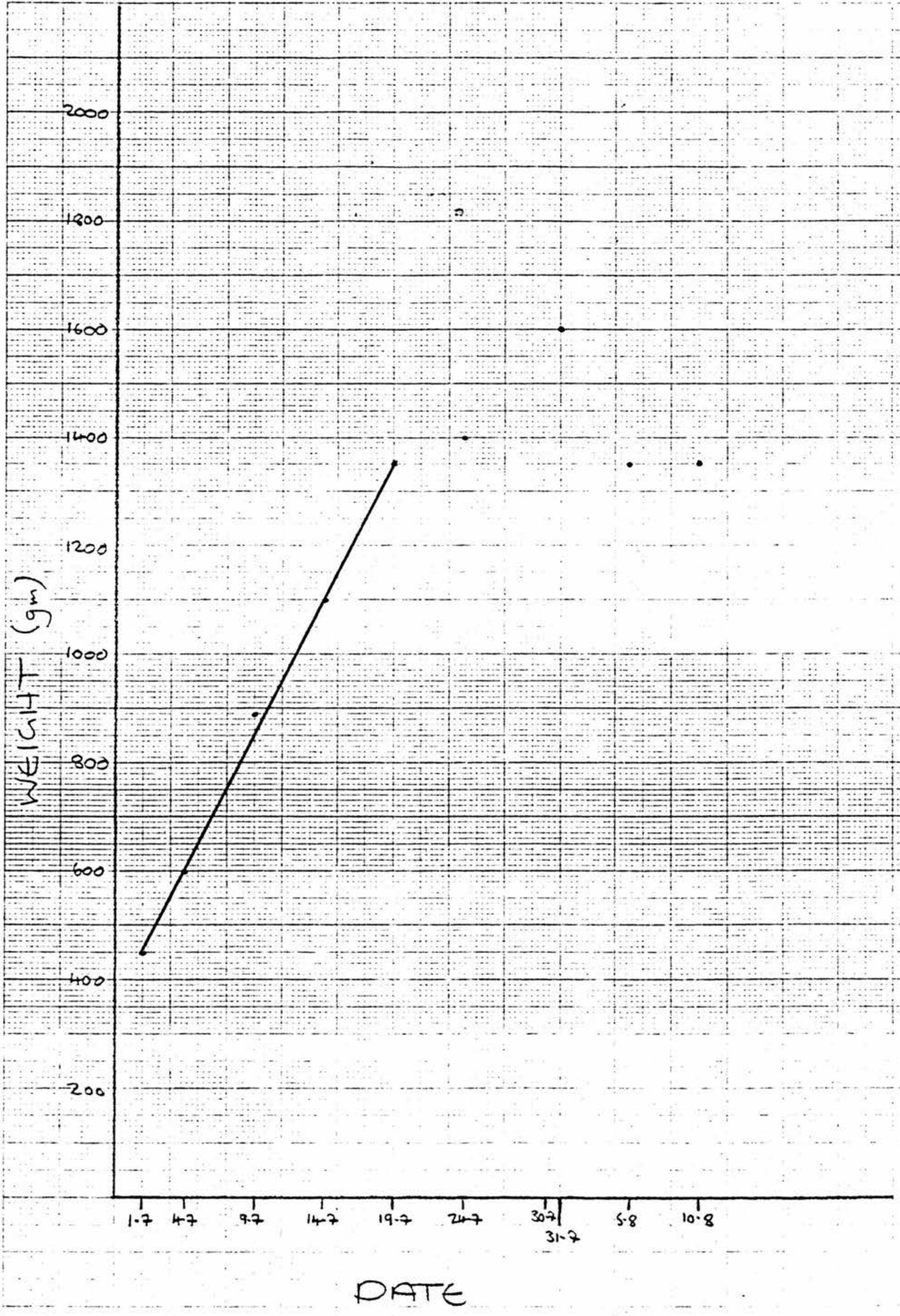
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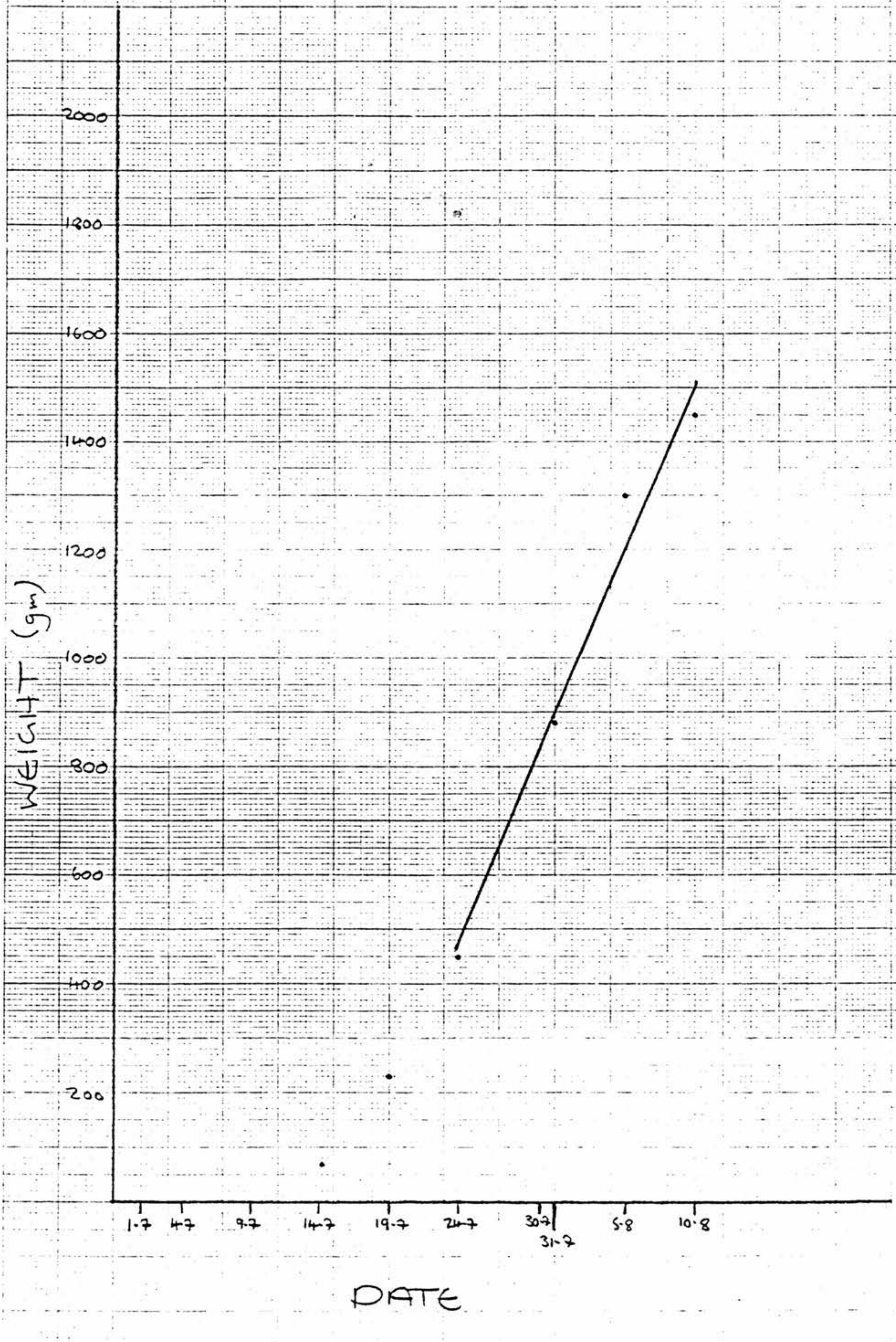
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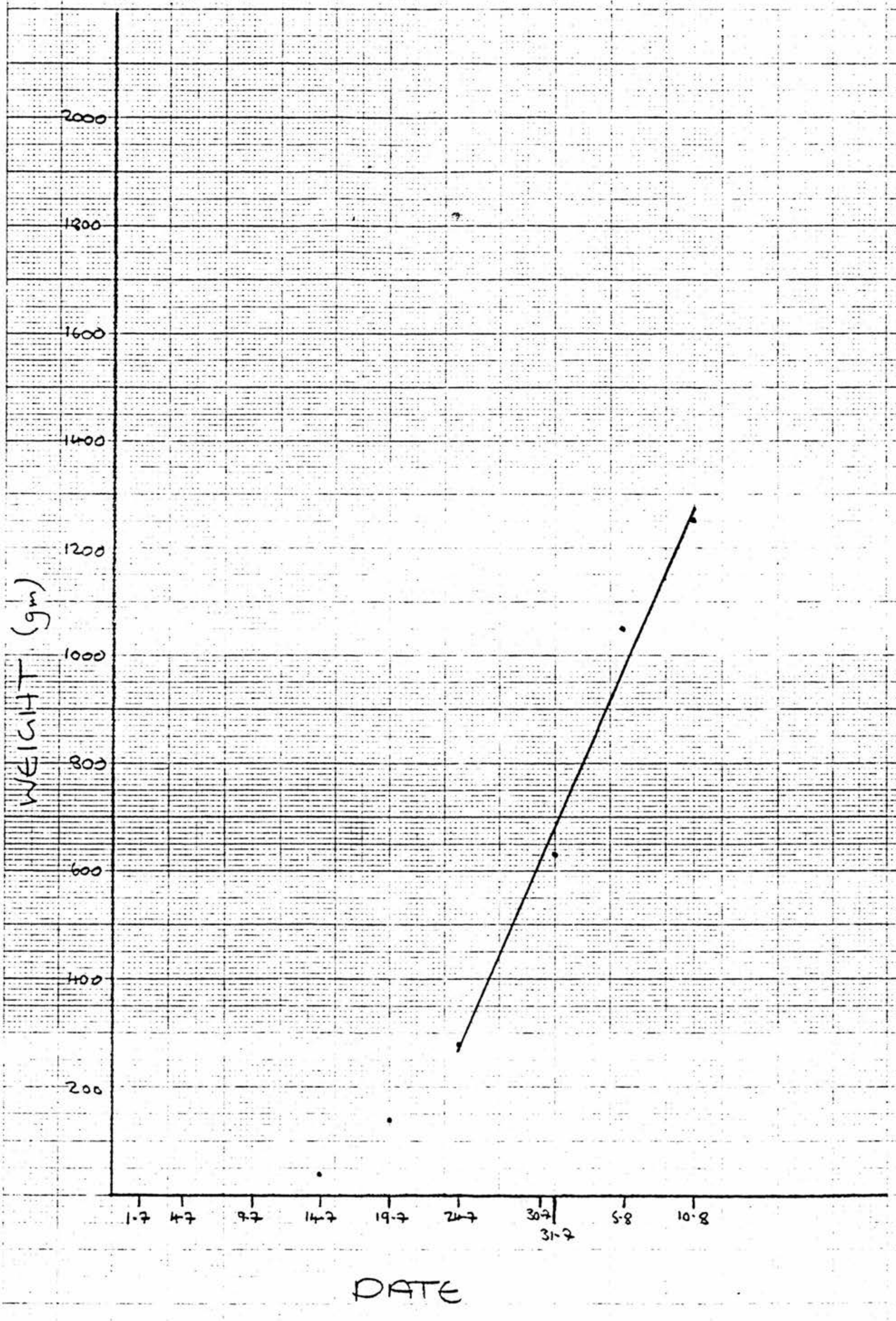

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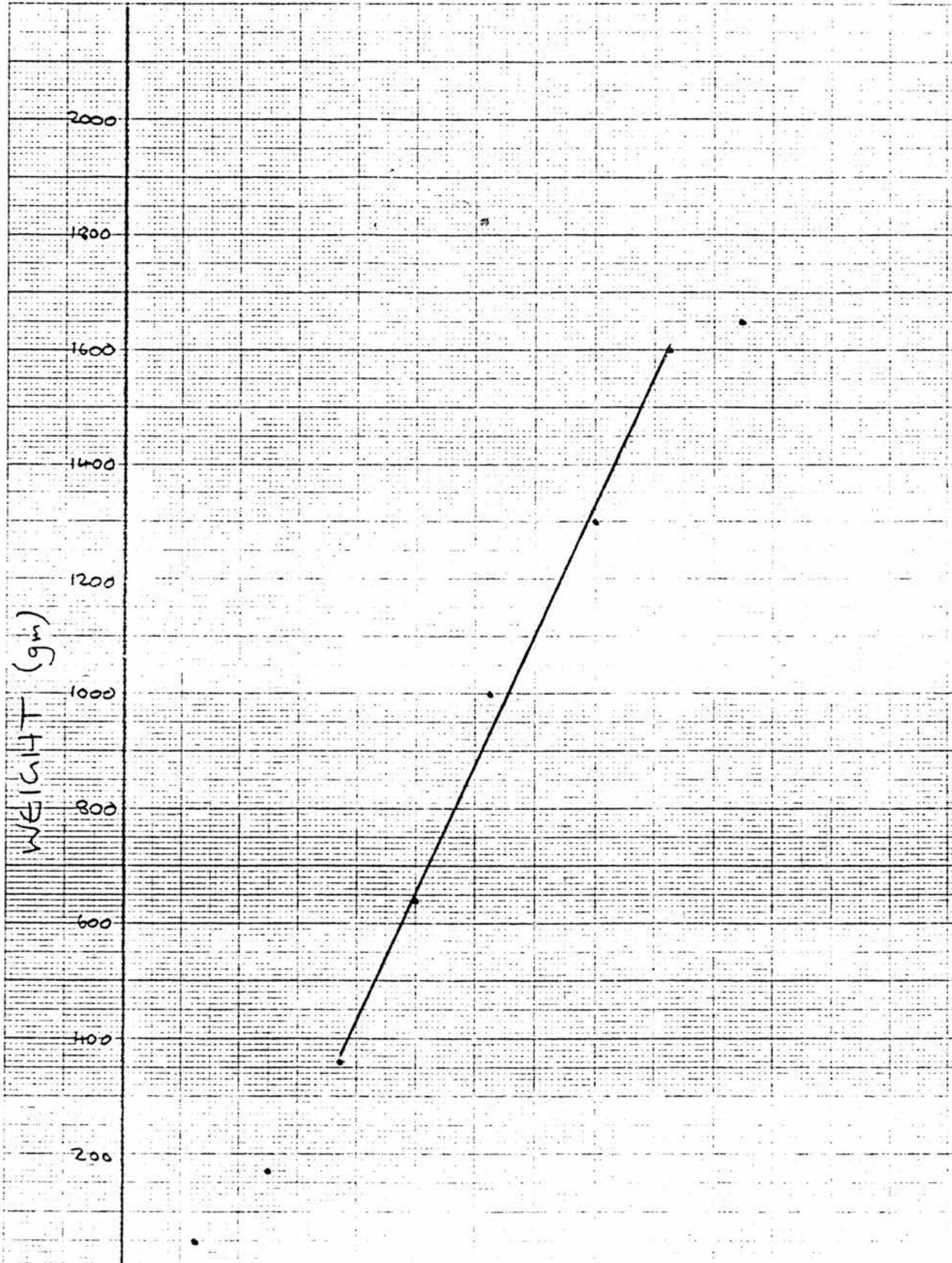

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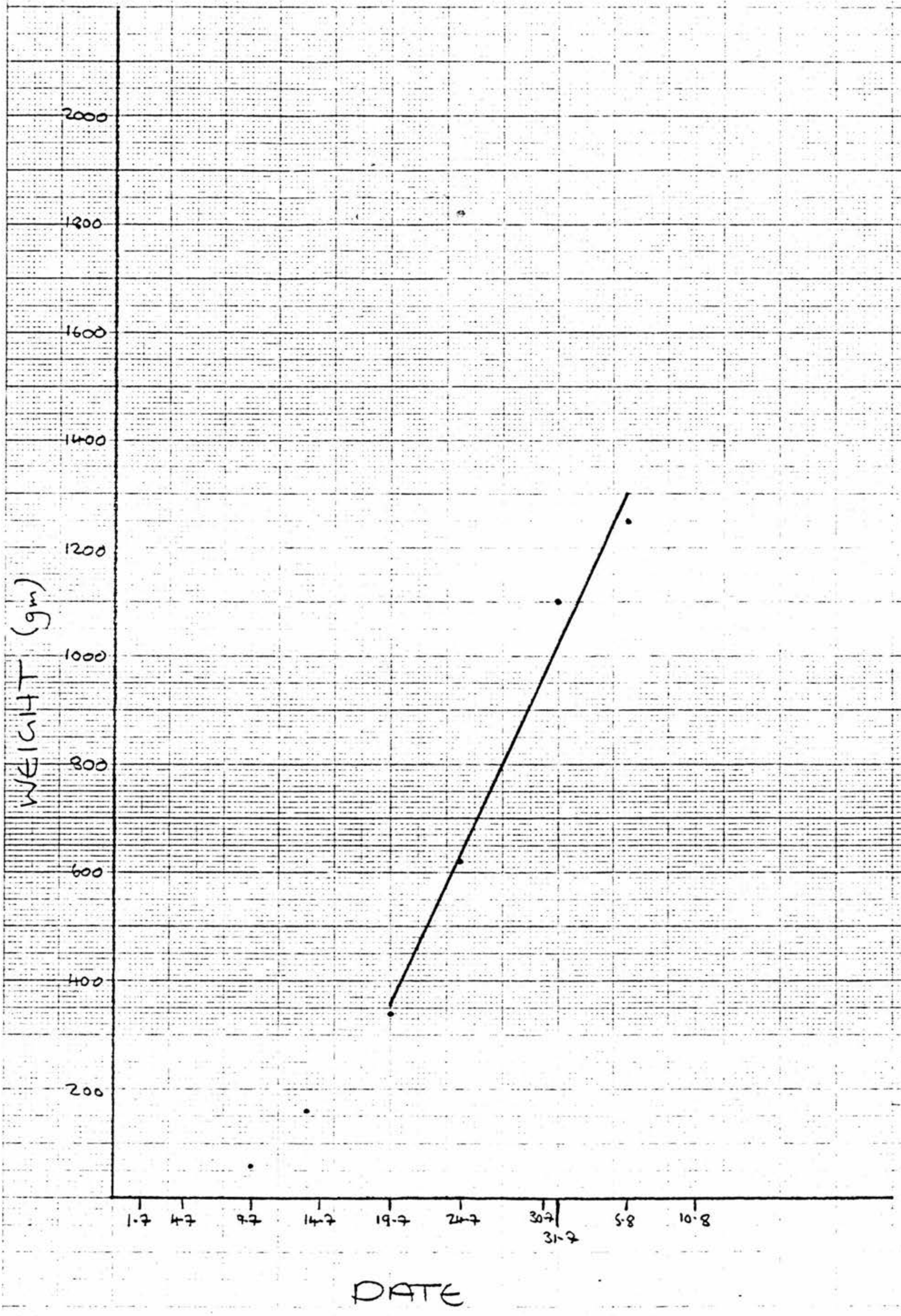
16 #2

NB. THIS CHICK DEAD ON 10-8-86



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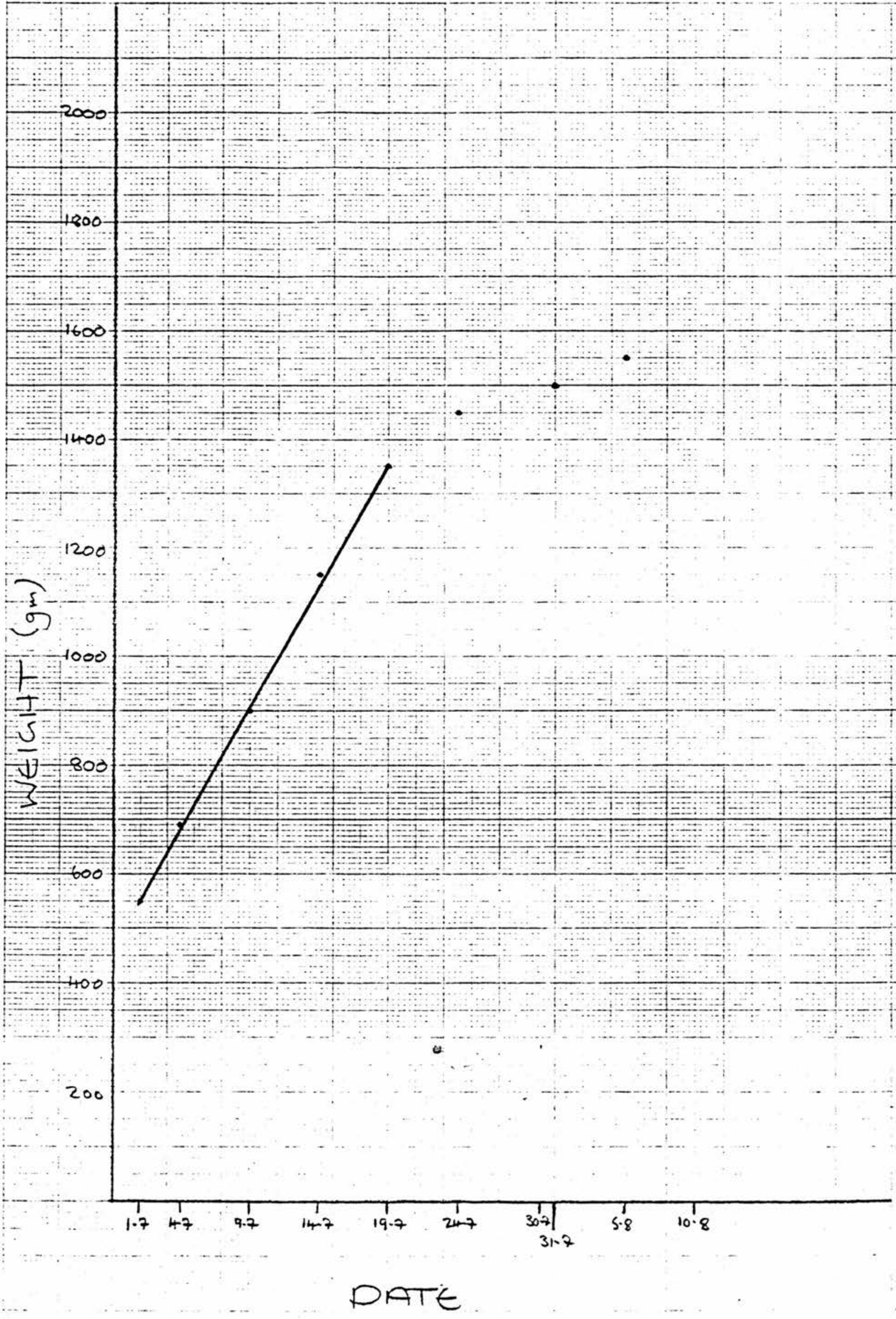

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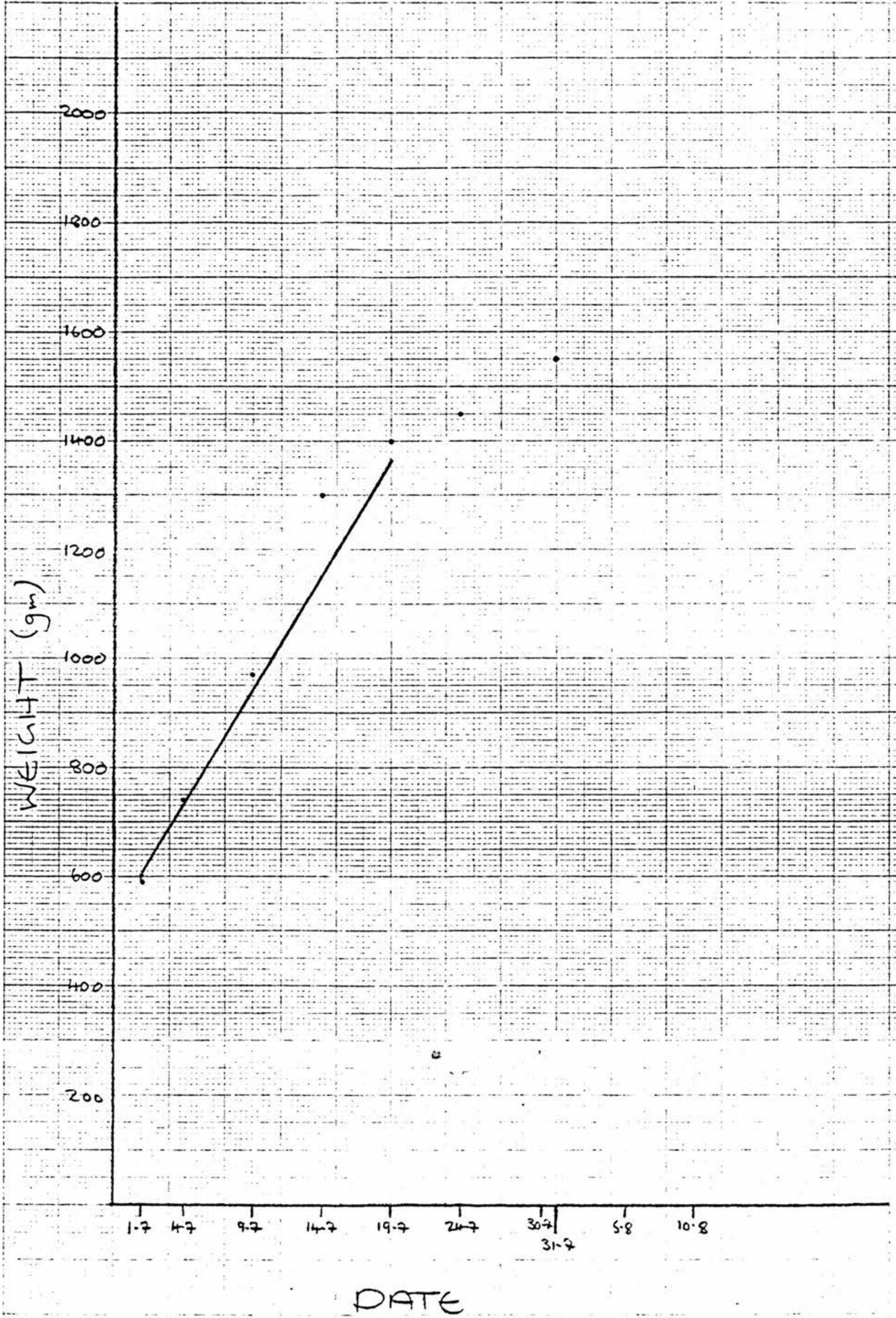
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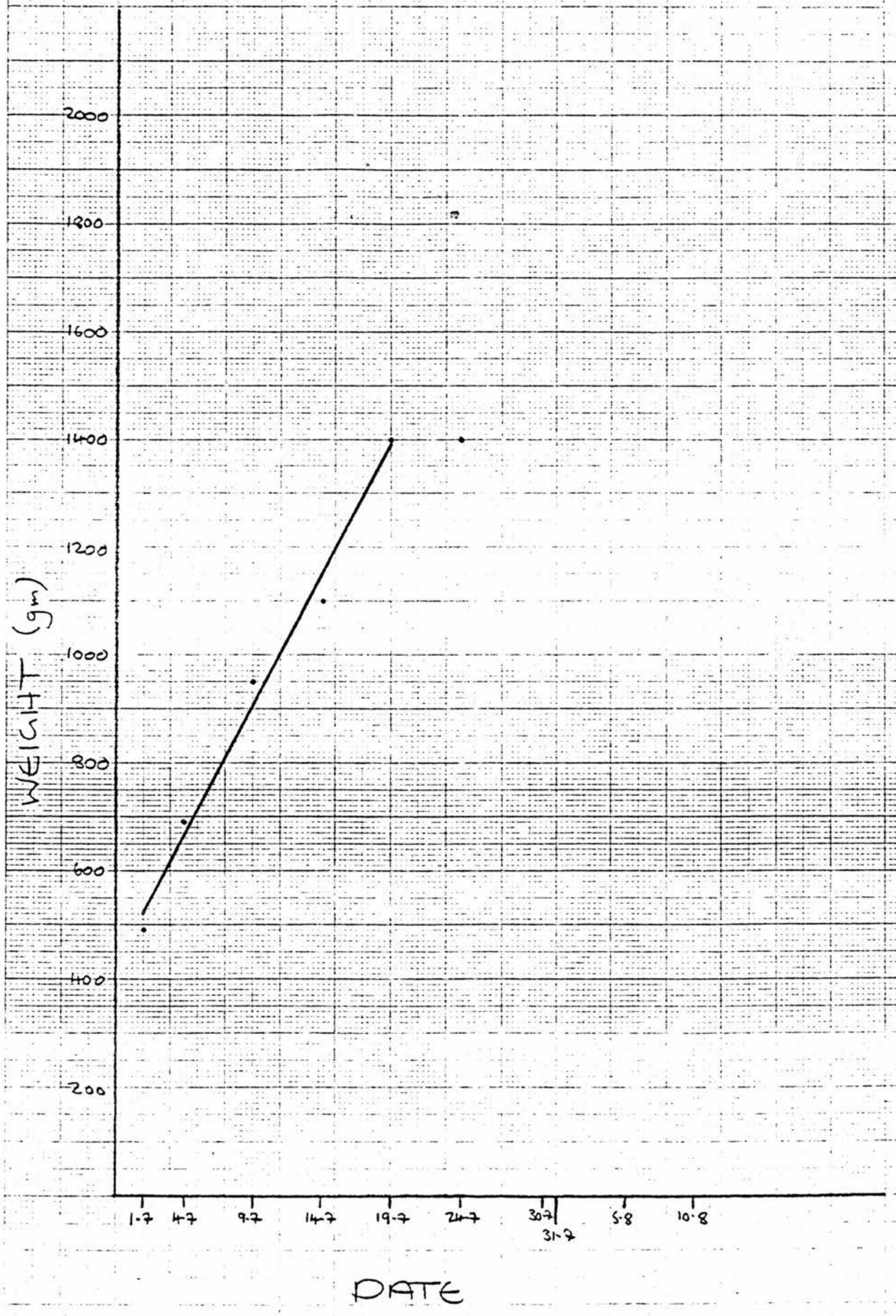

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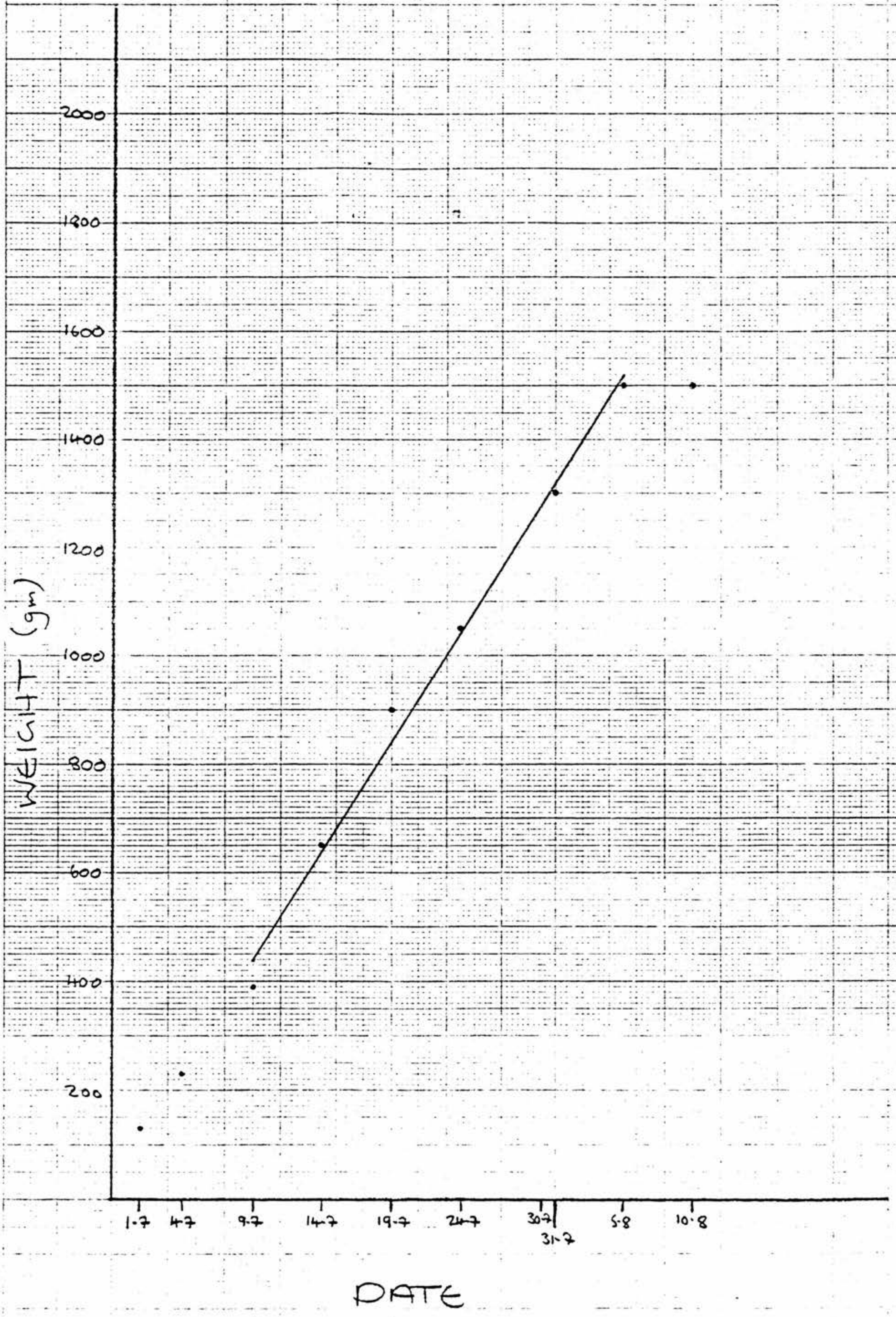

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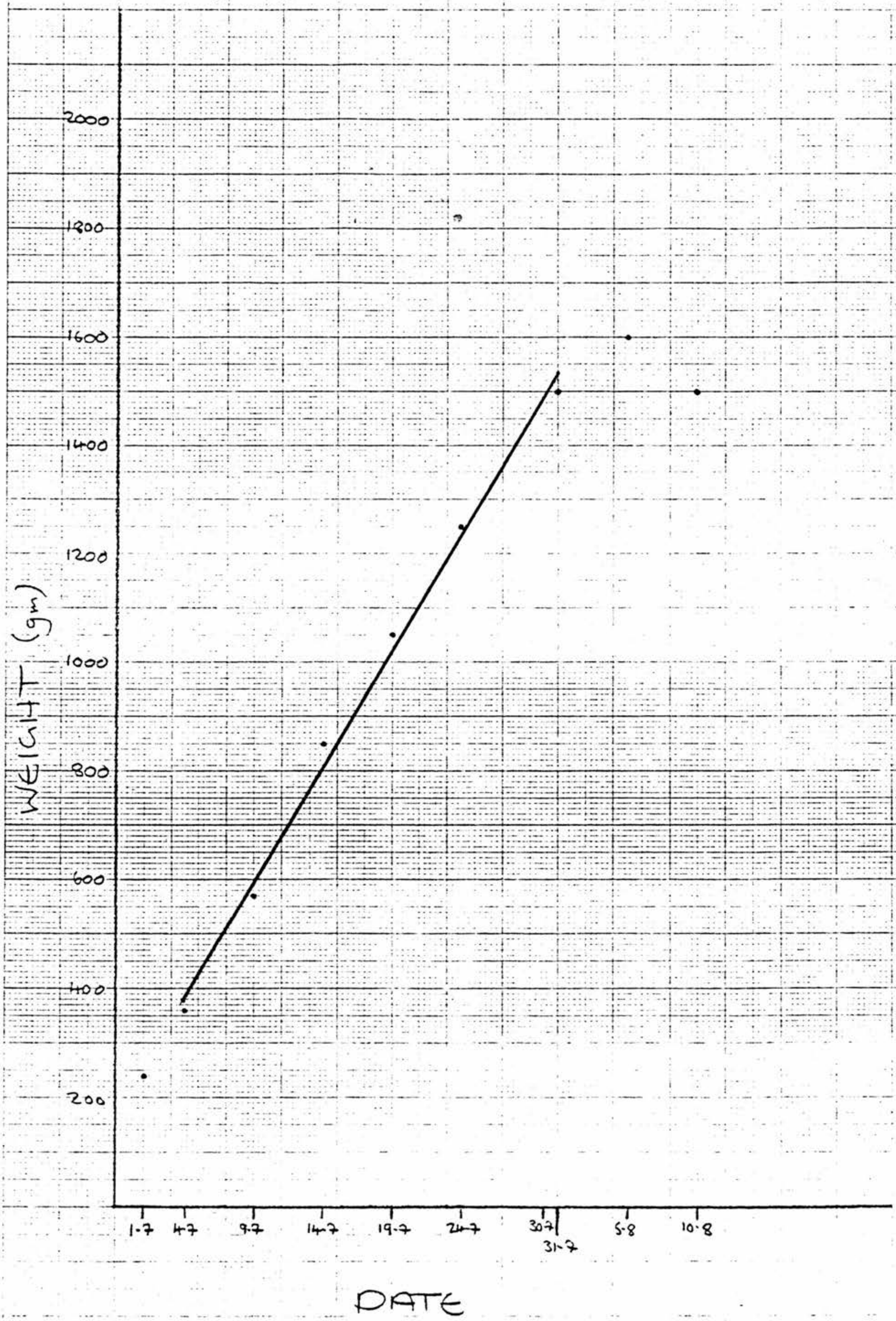
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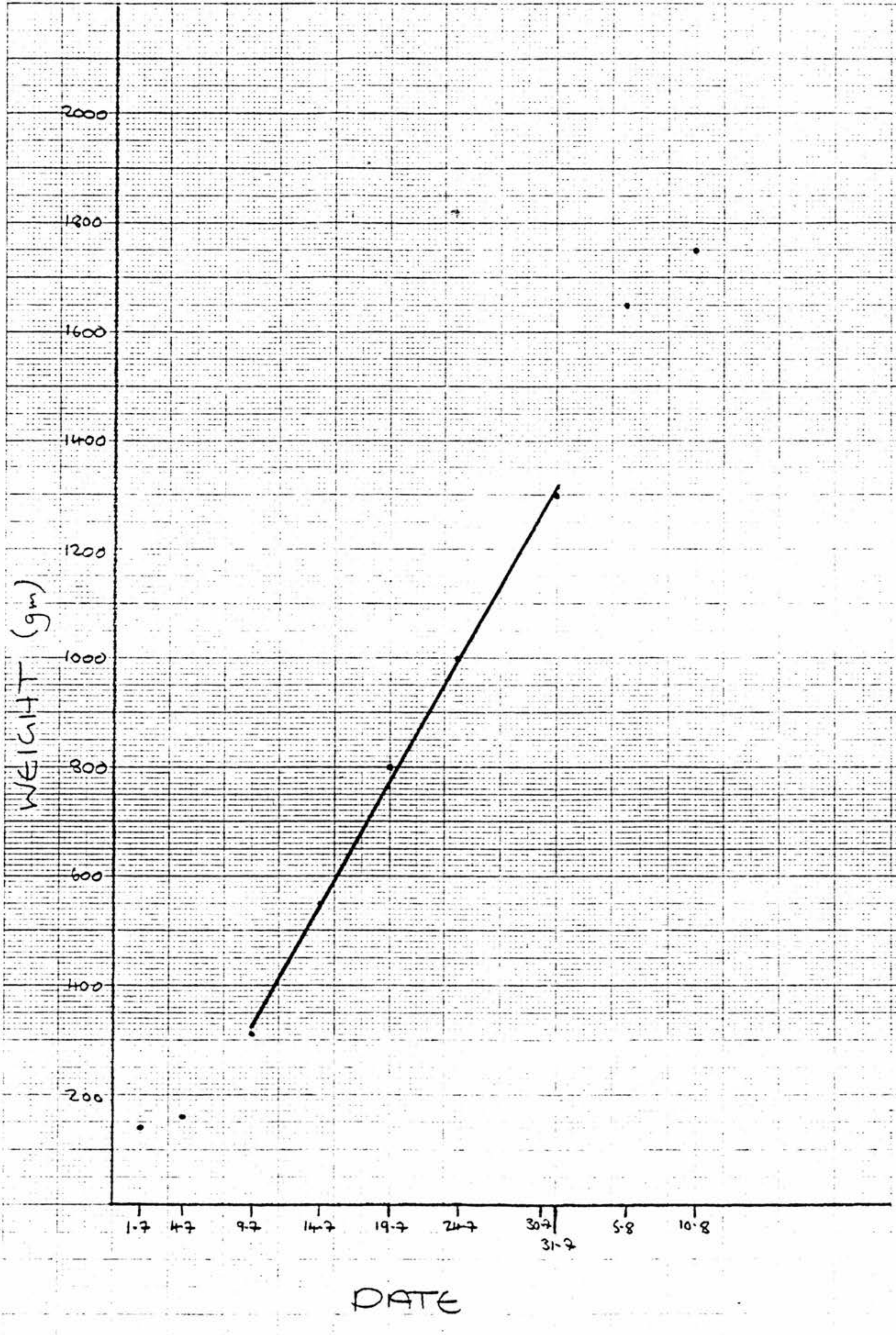
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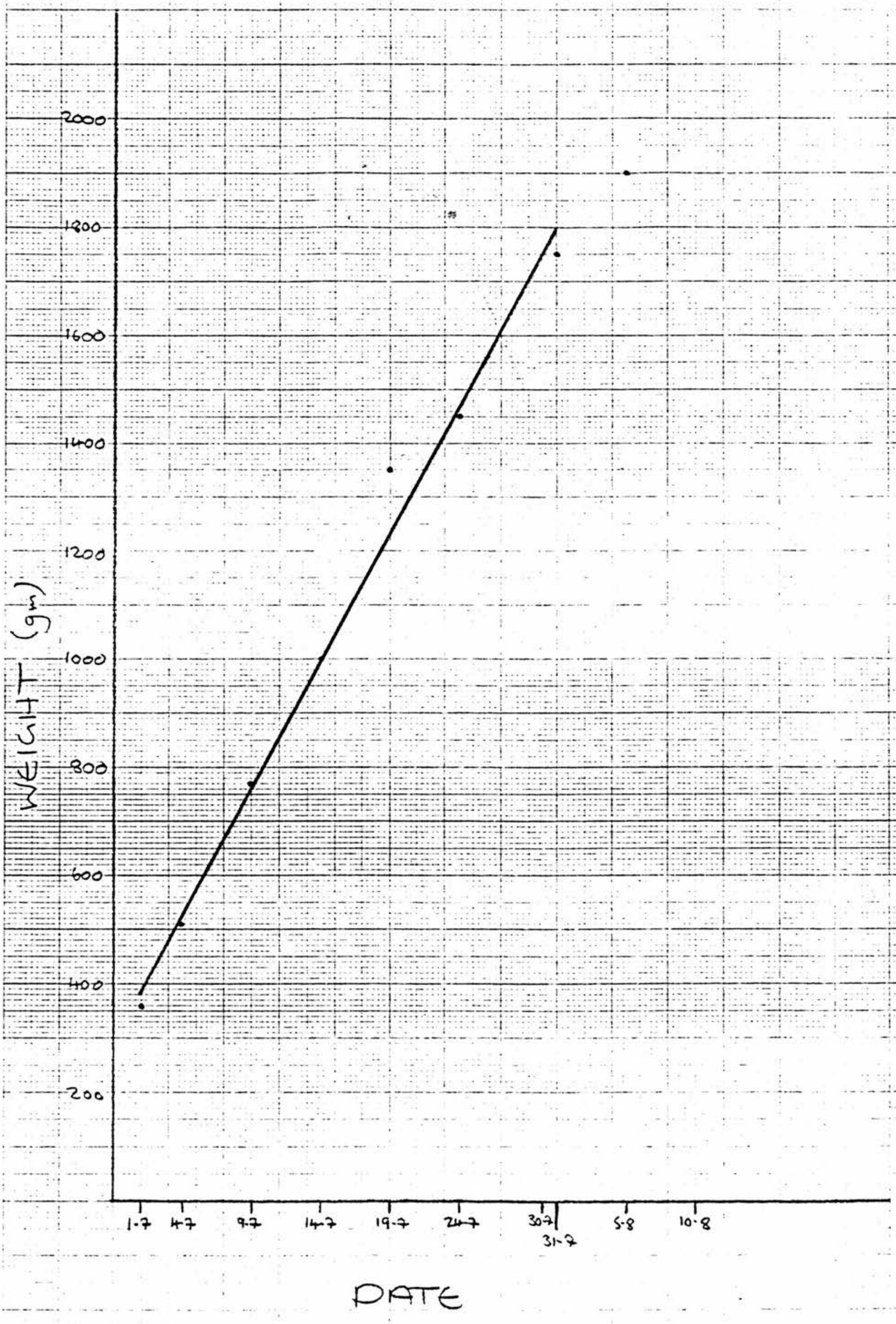
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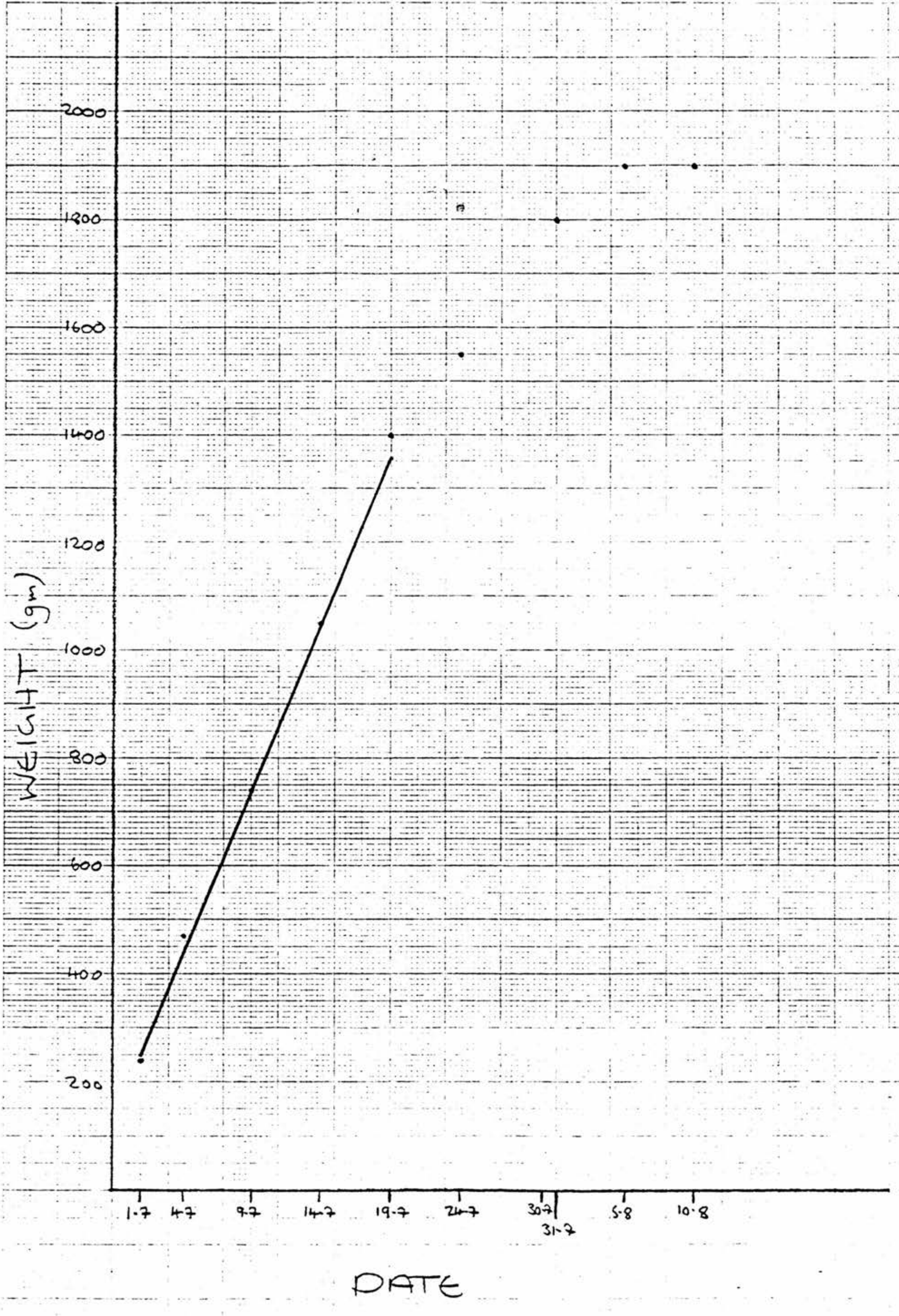
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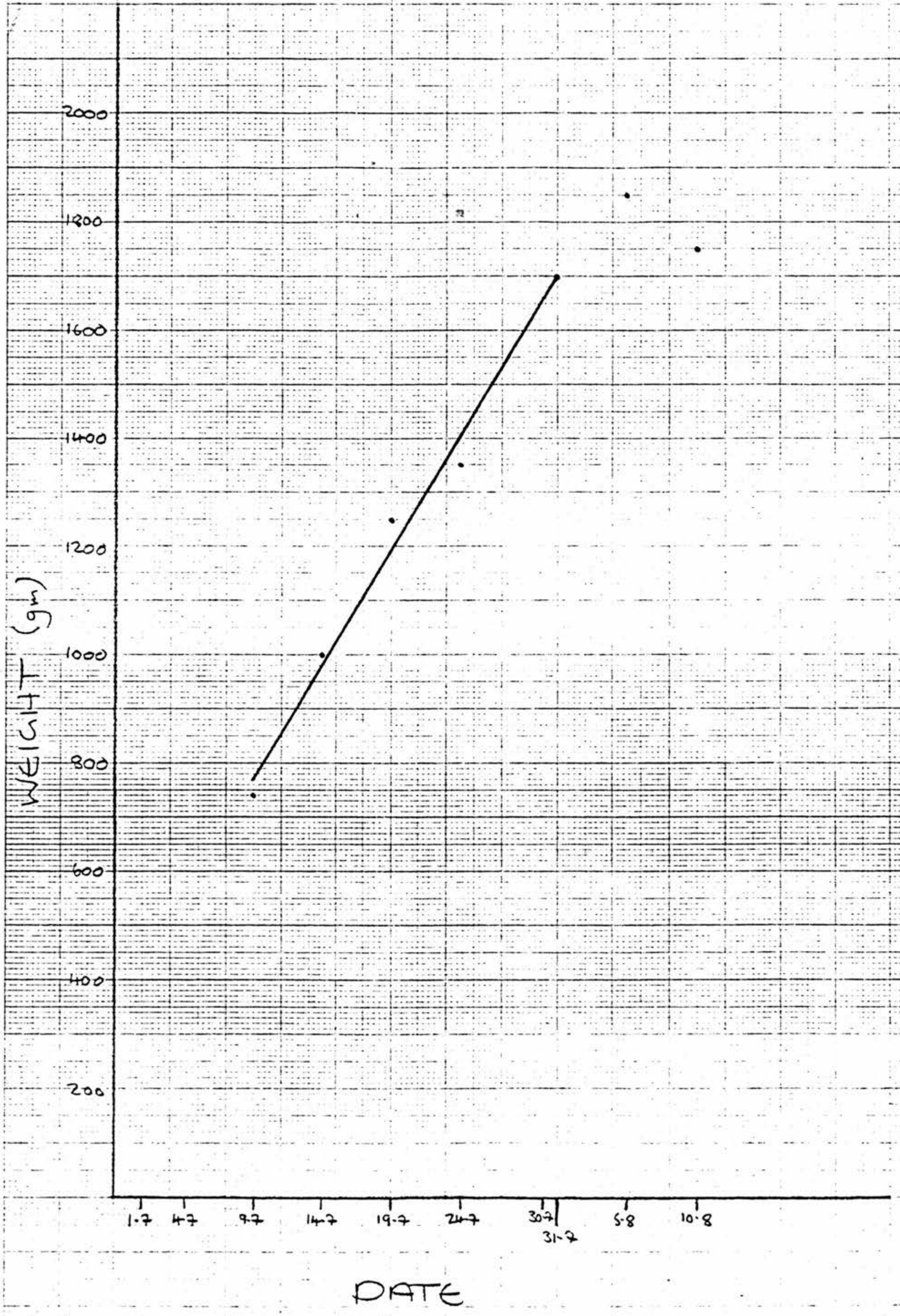

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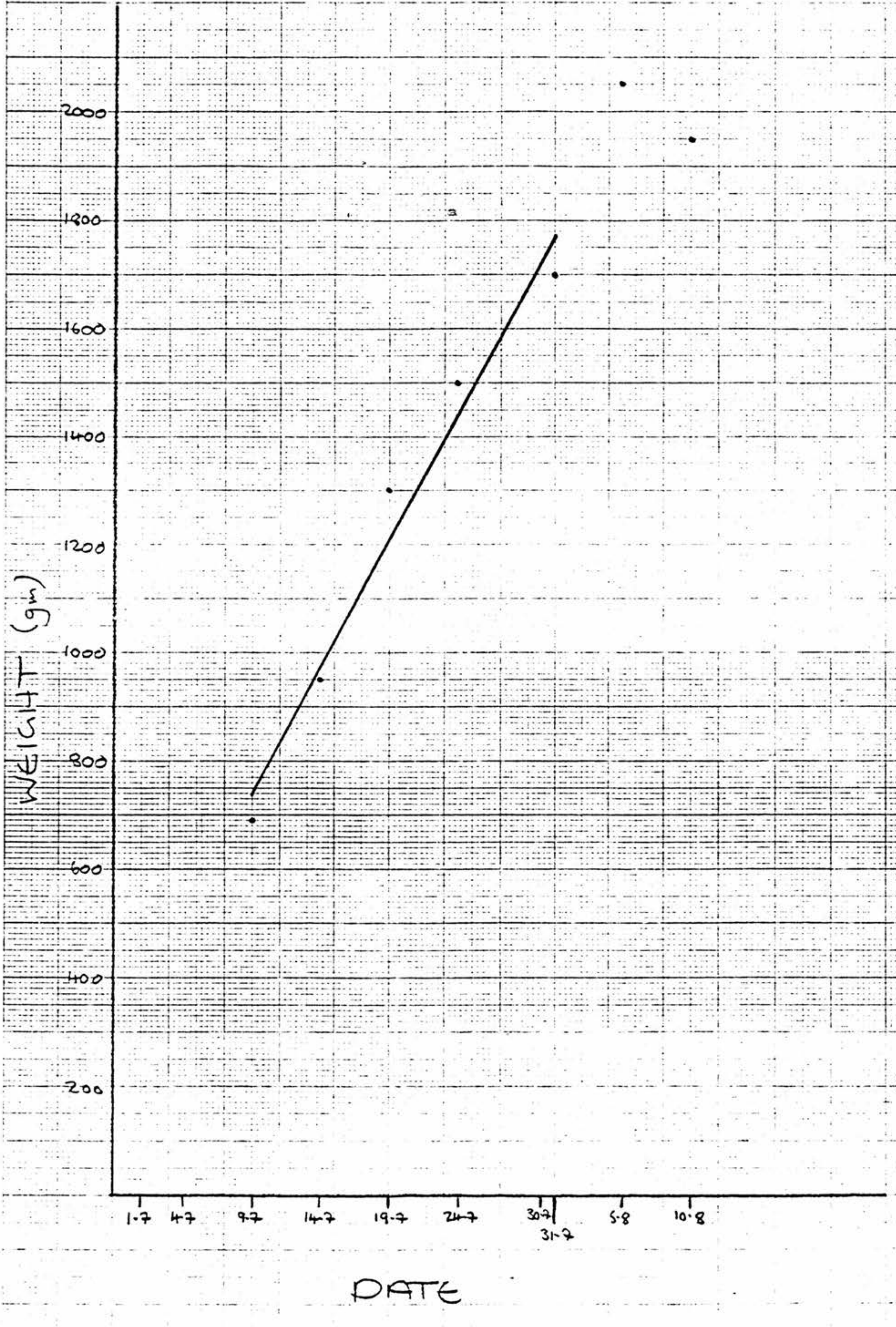
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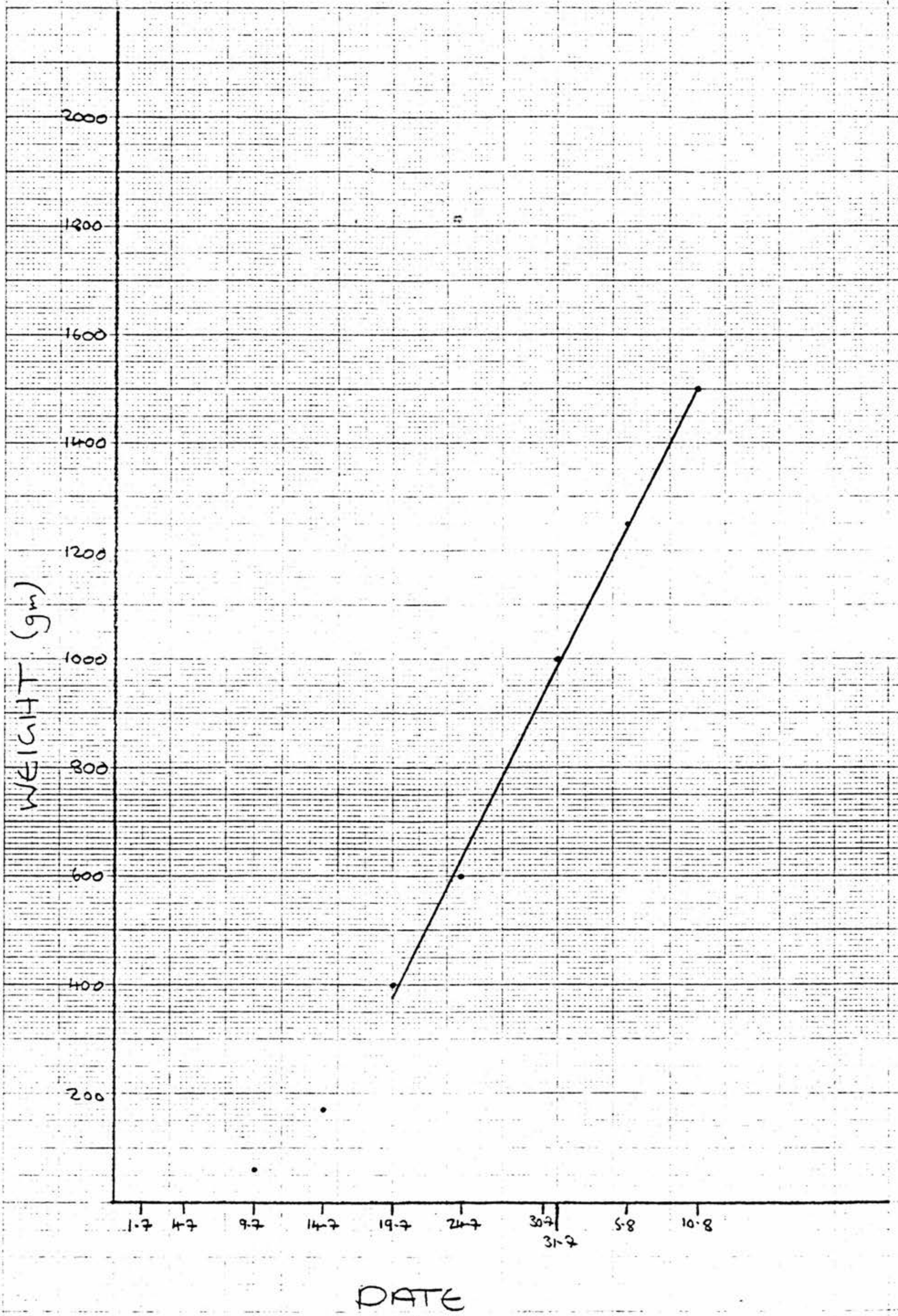
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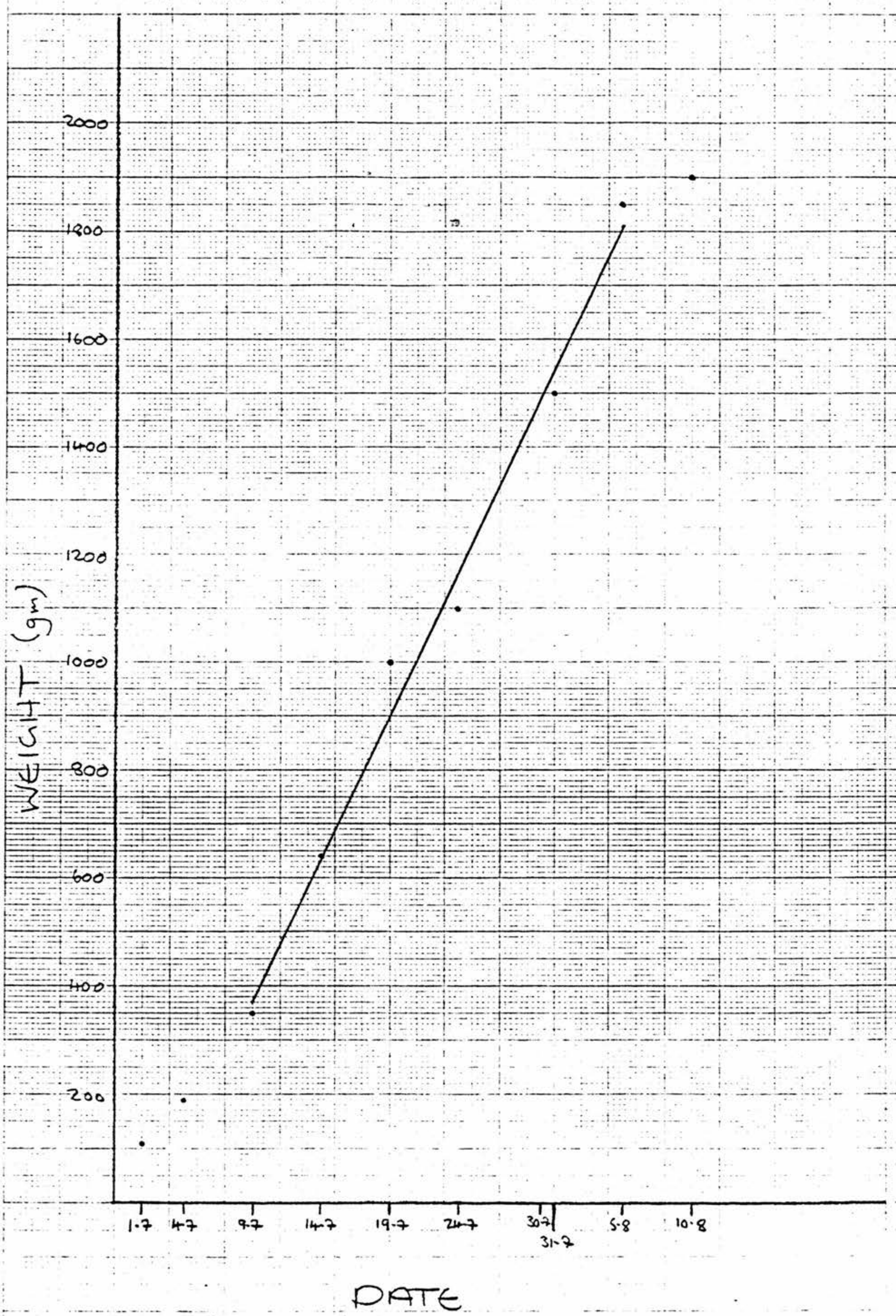
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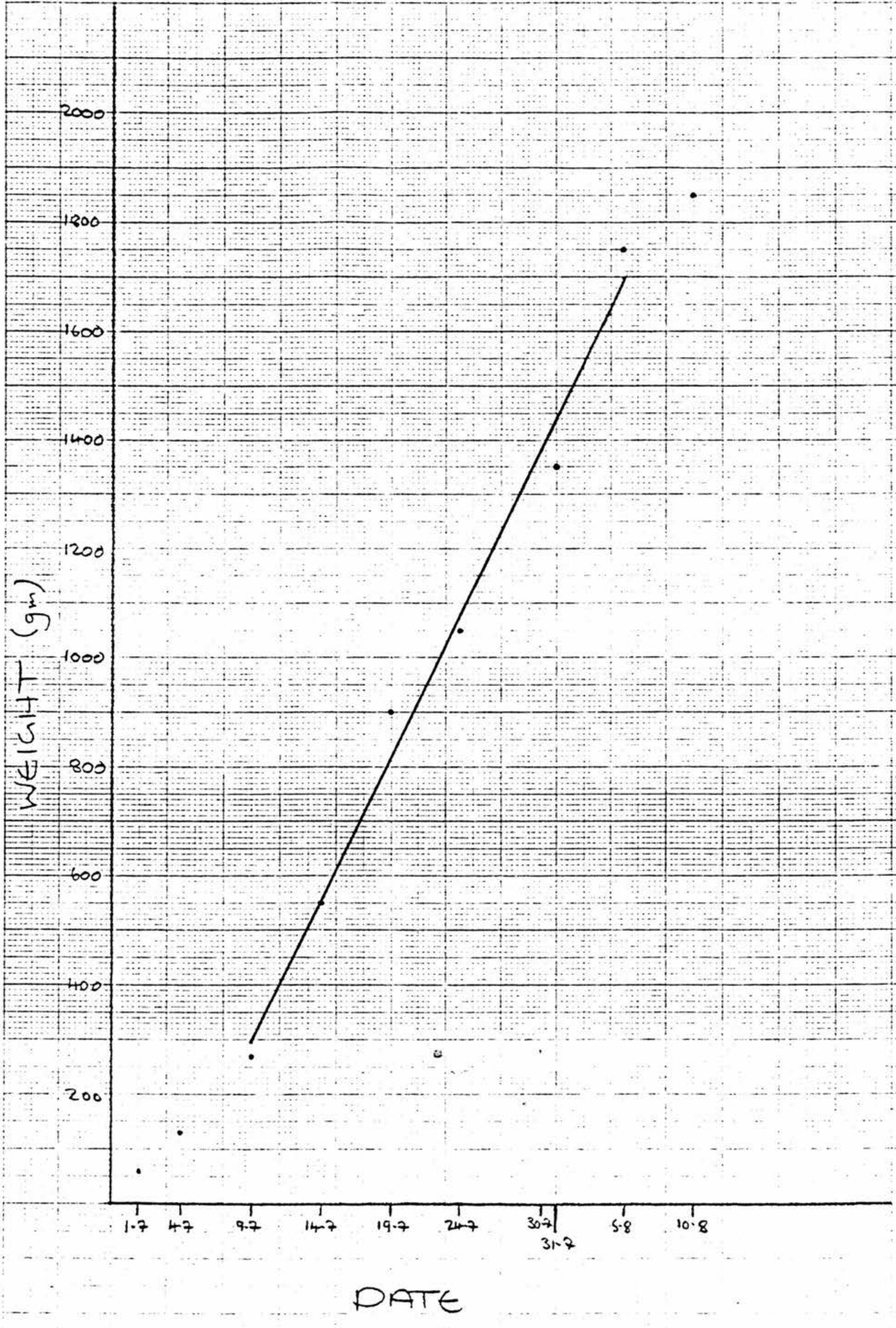

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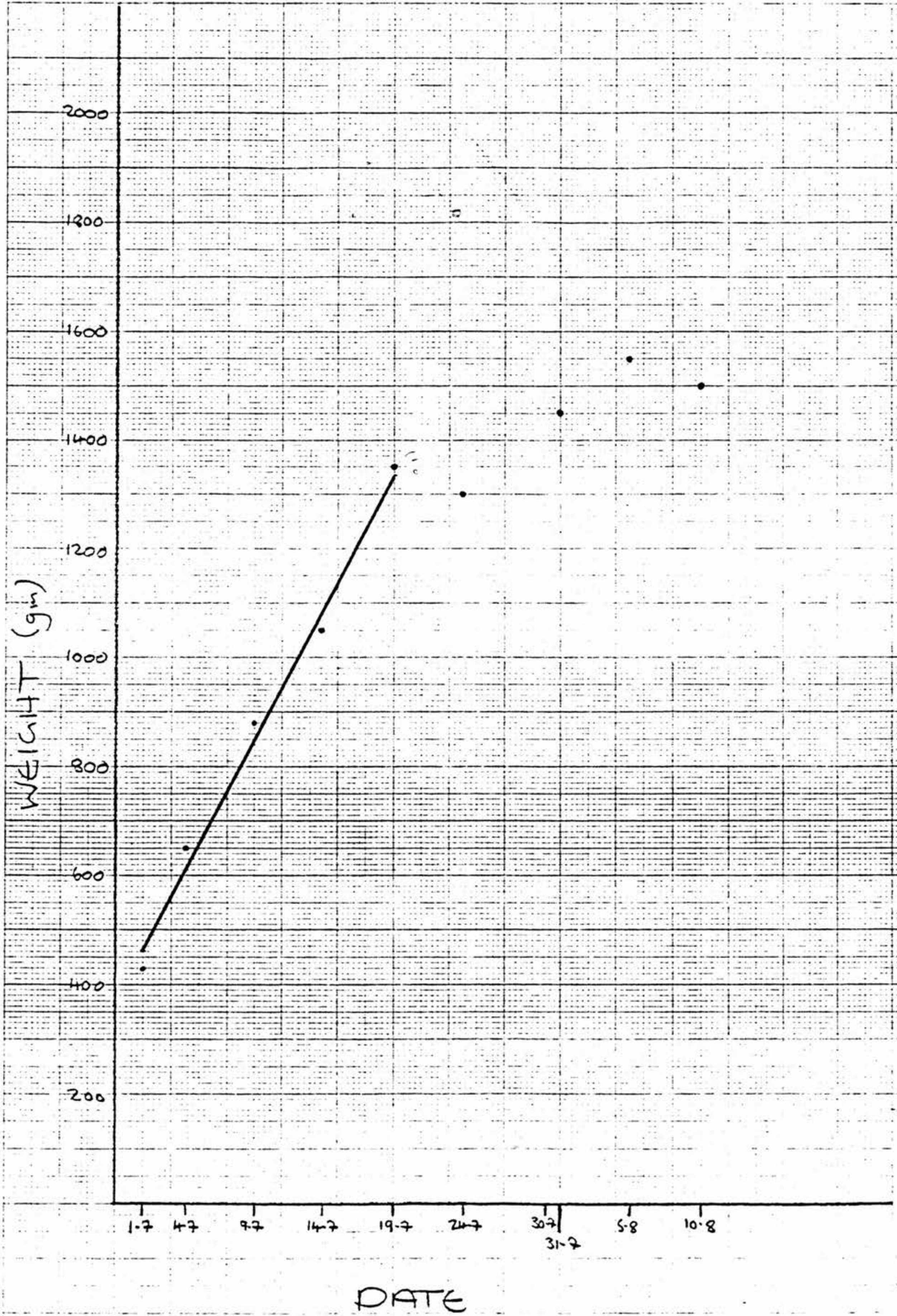
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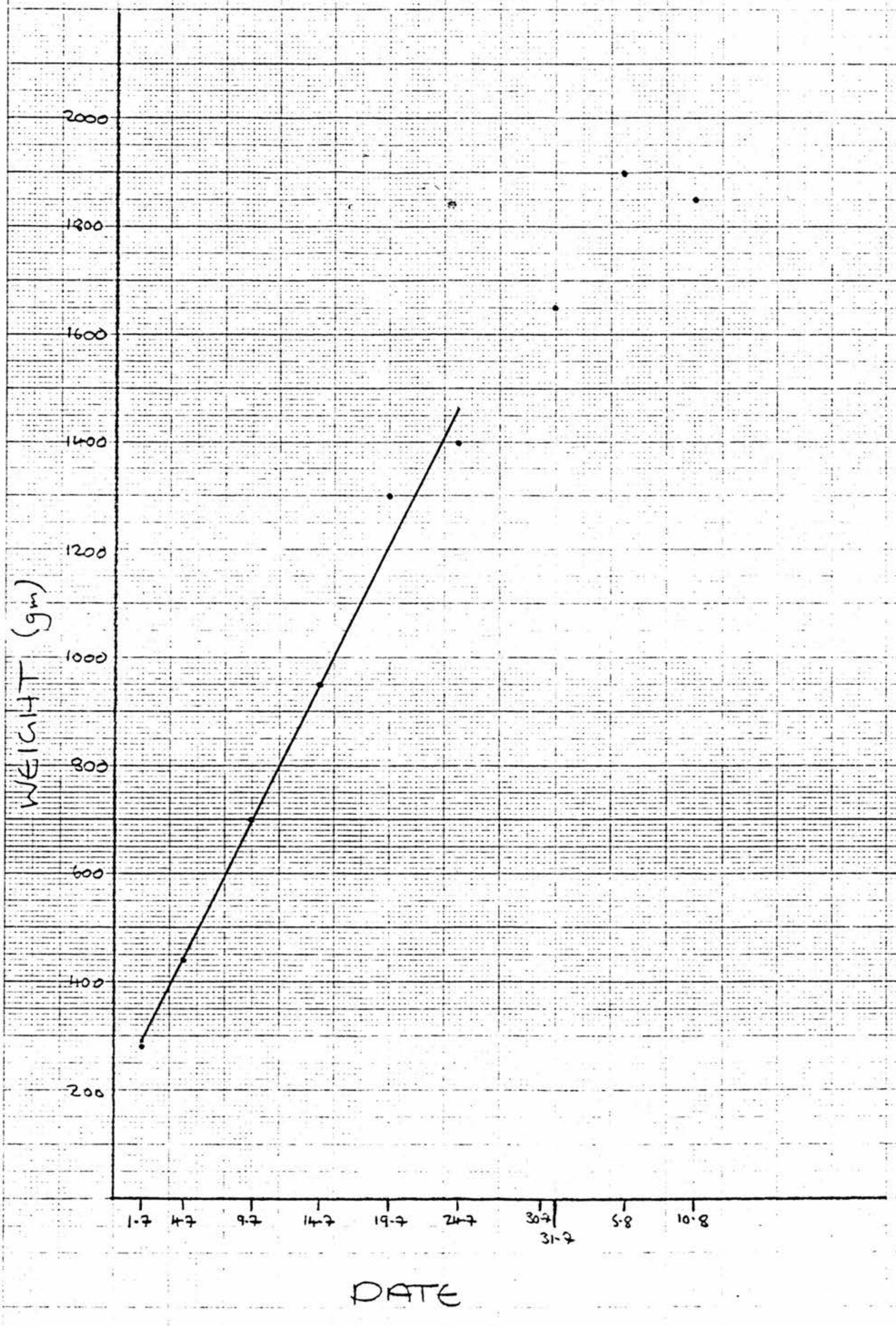
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5·8
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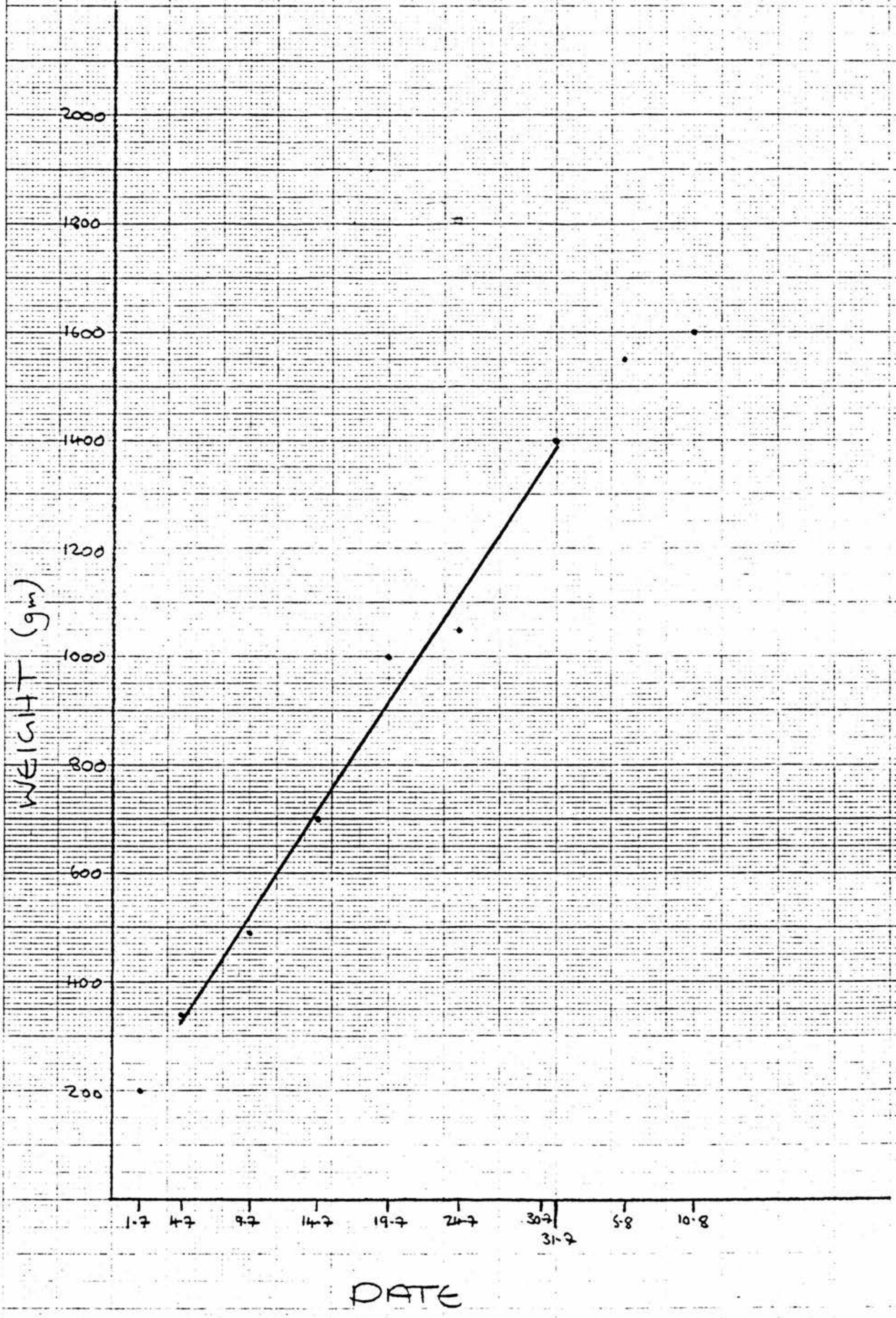
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5·8
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DATE

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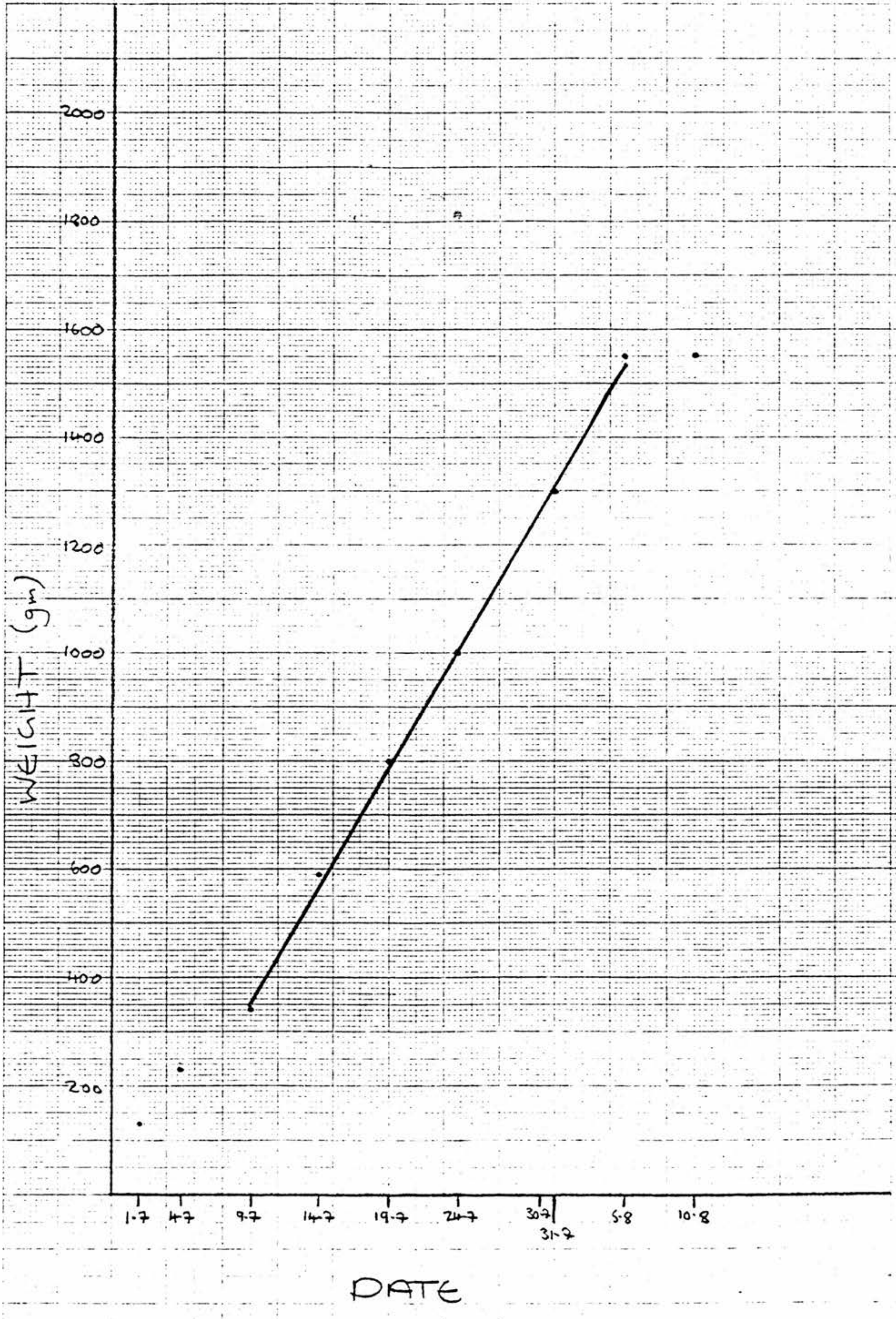
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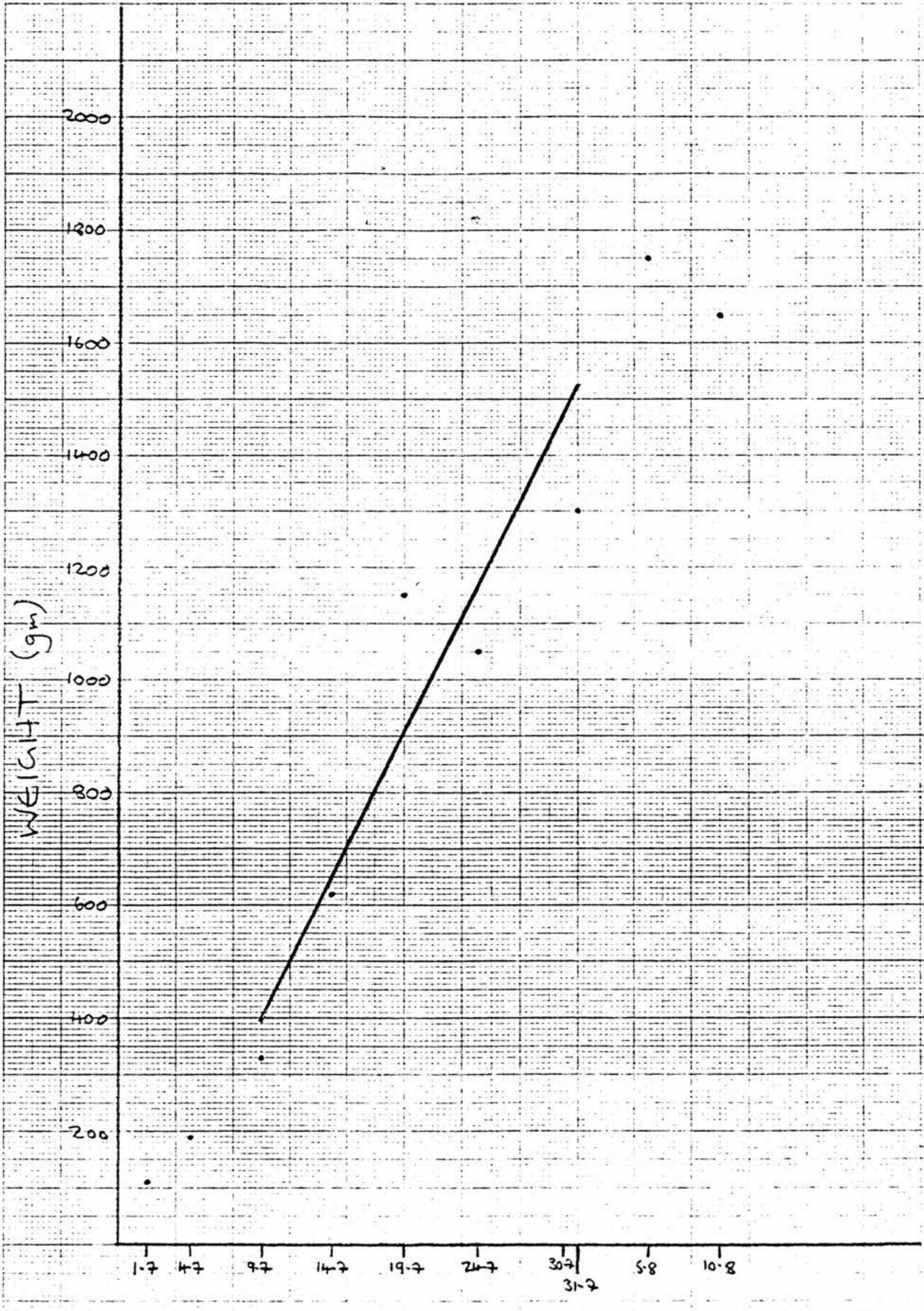
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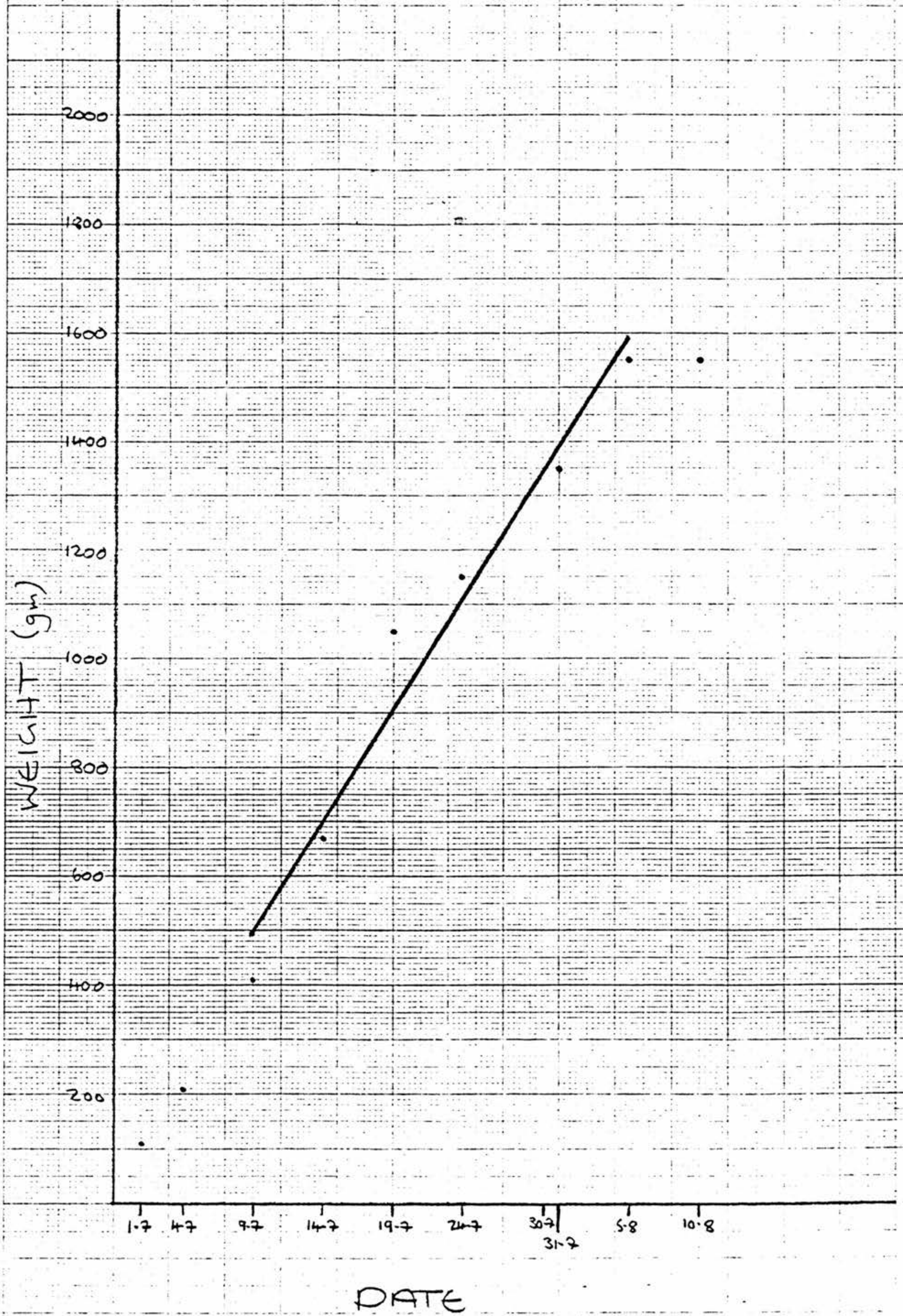
286 #1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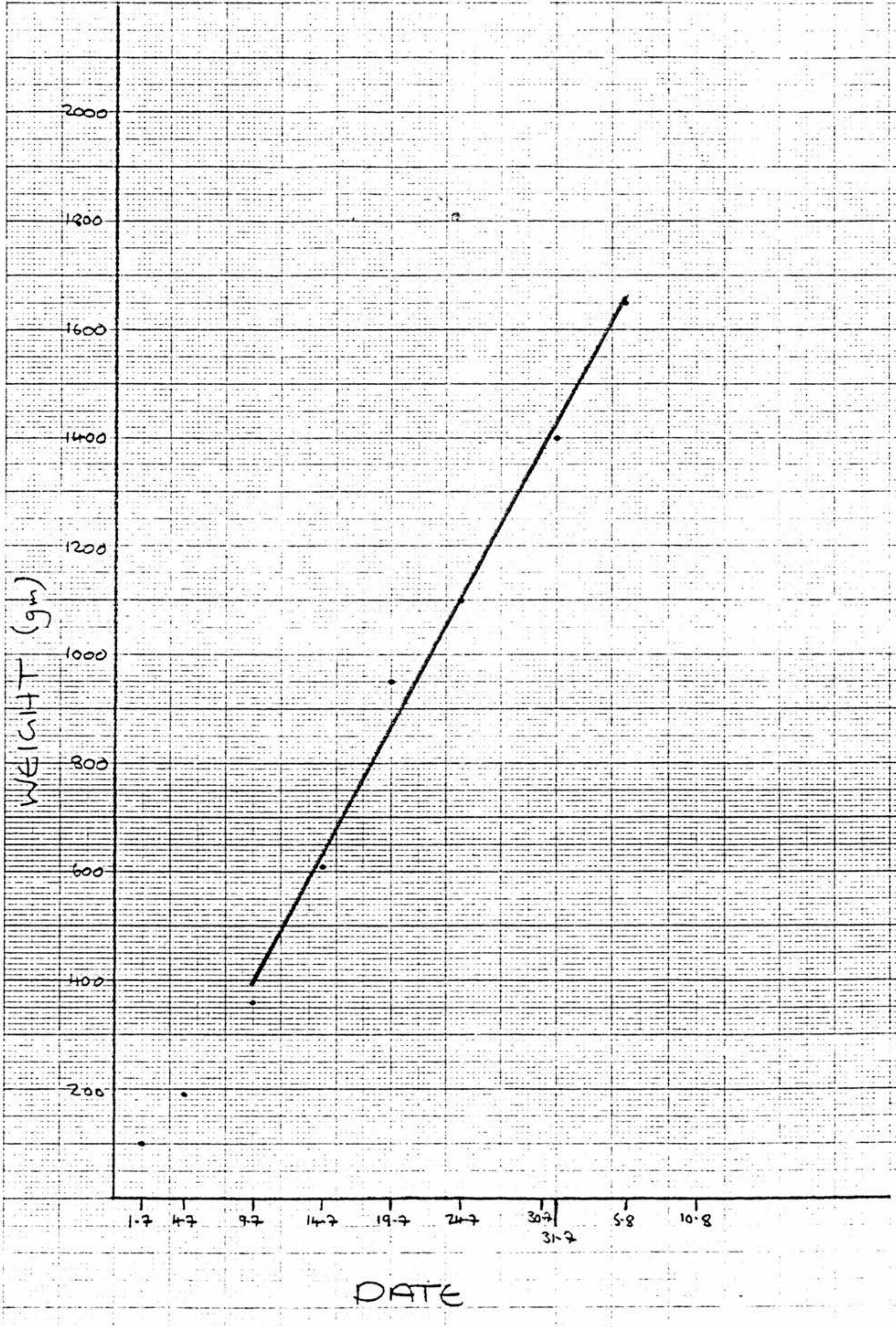
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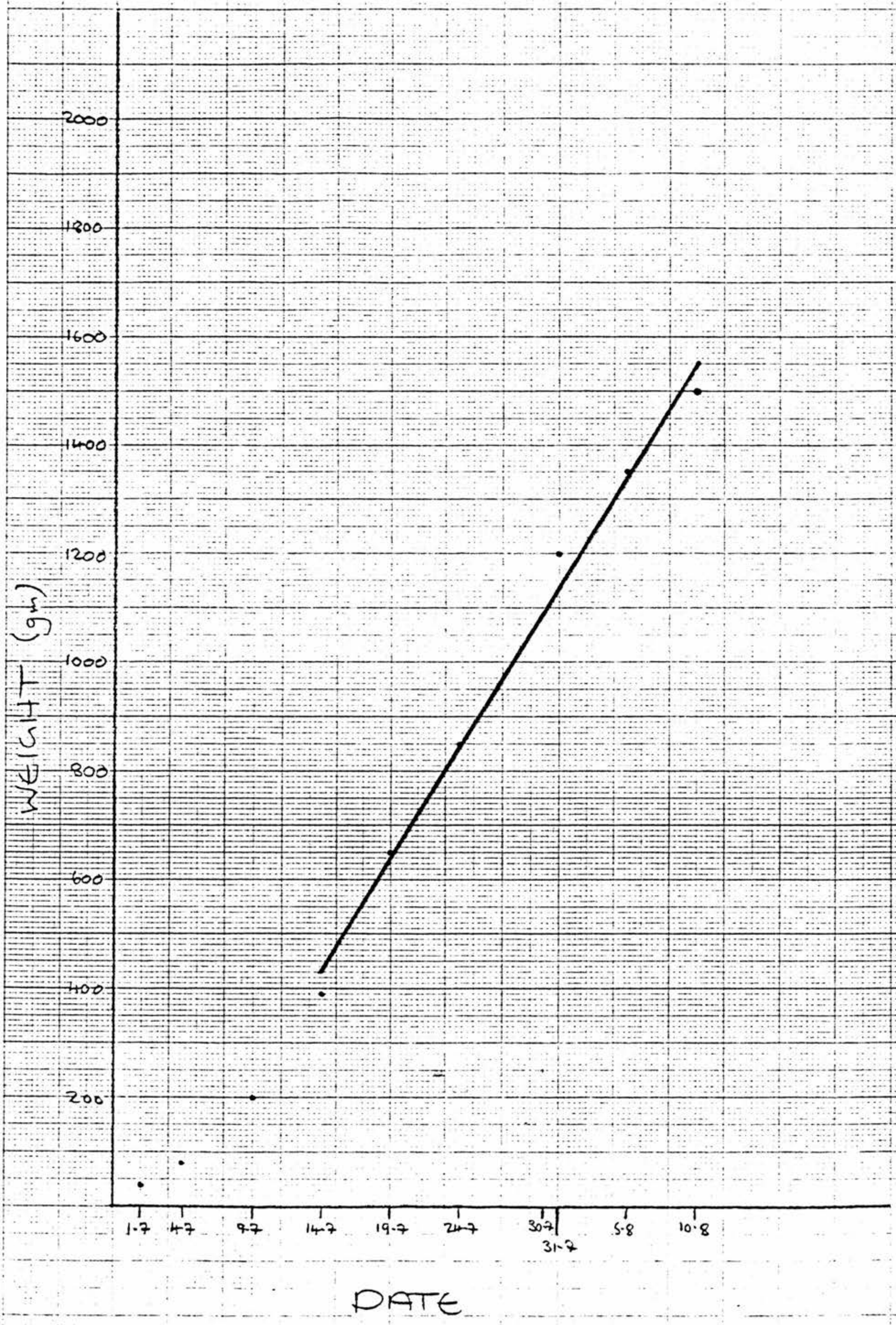

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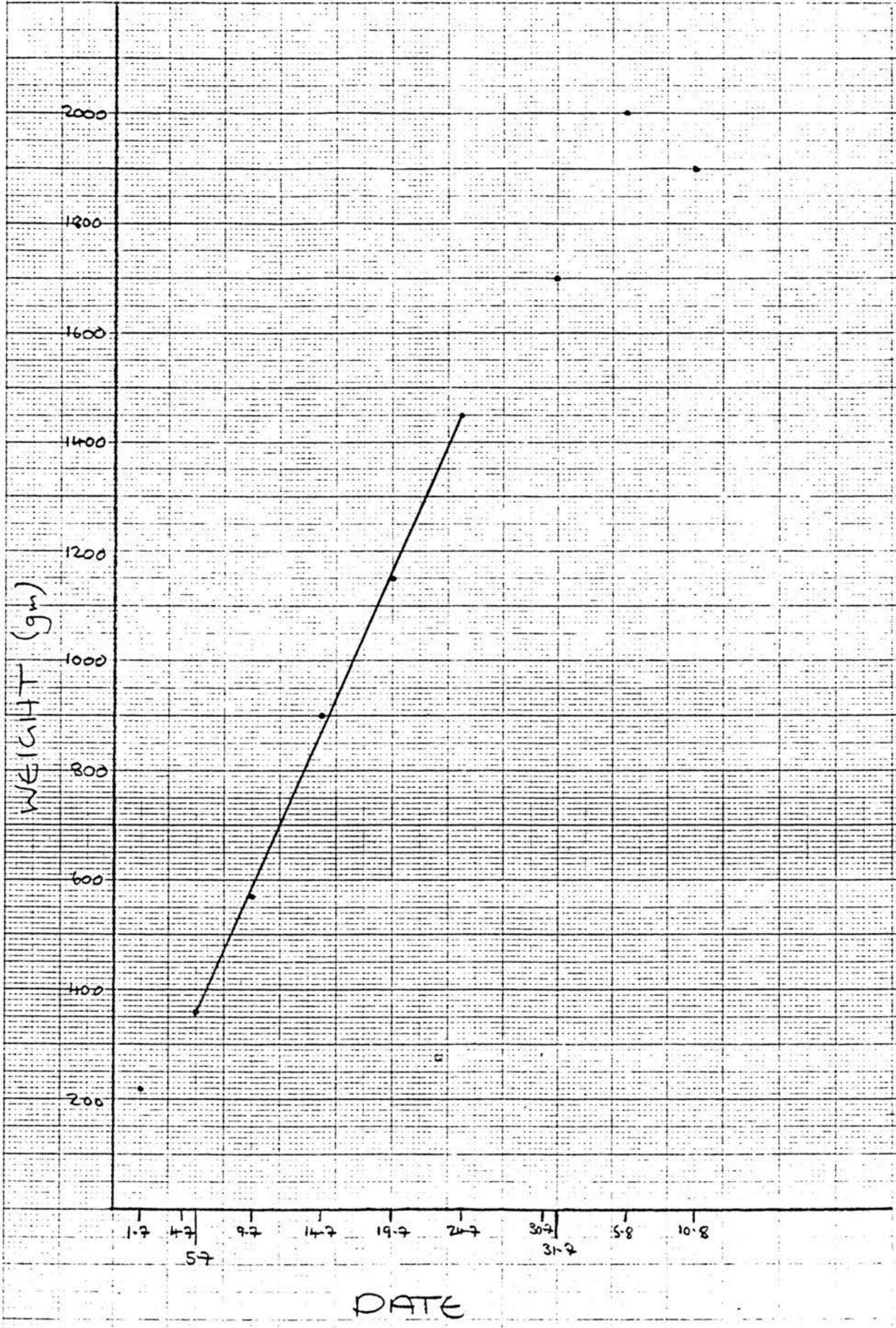
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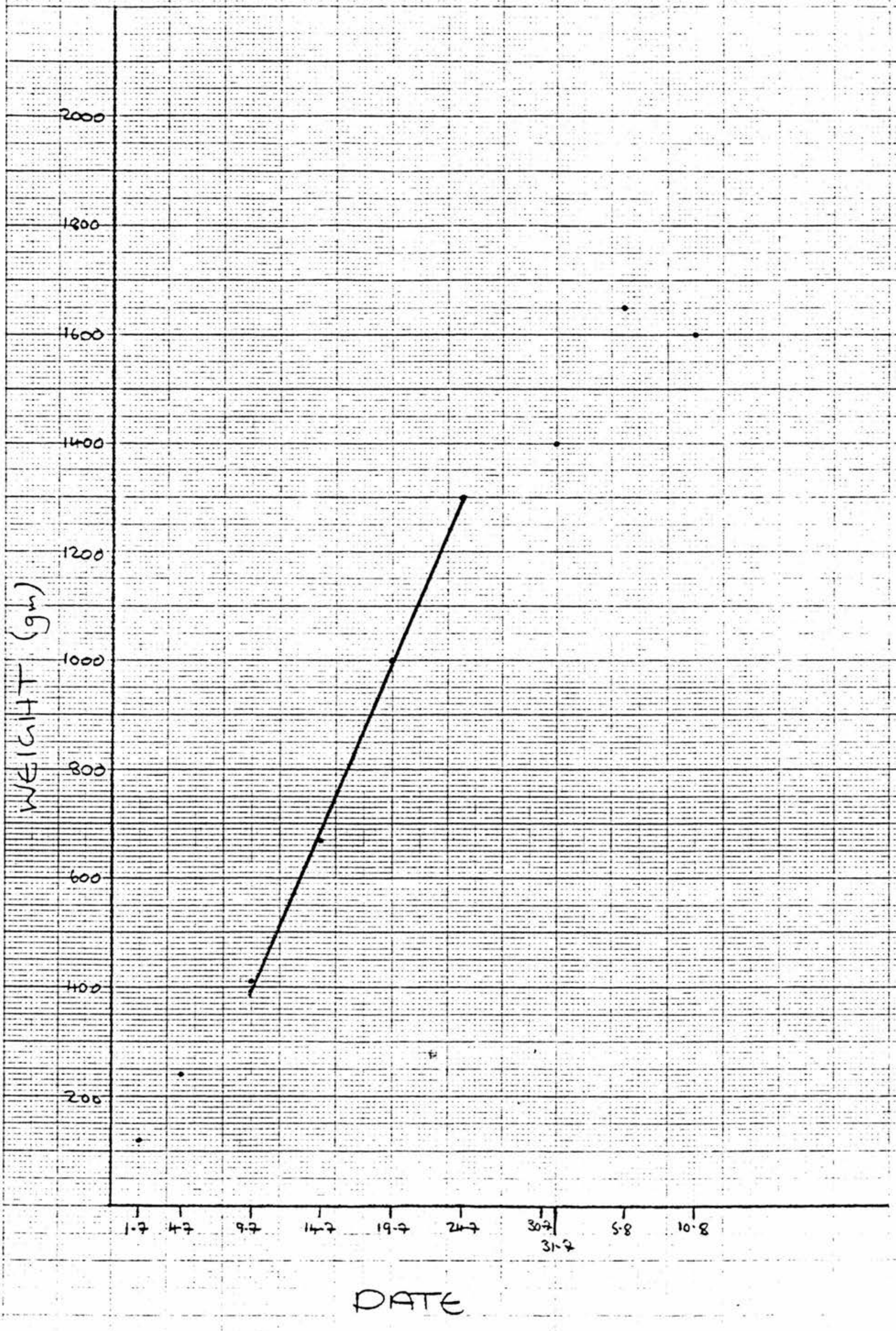
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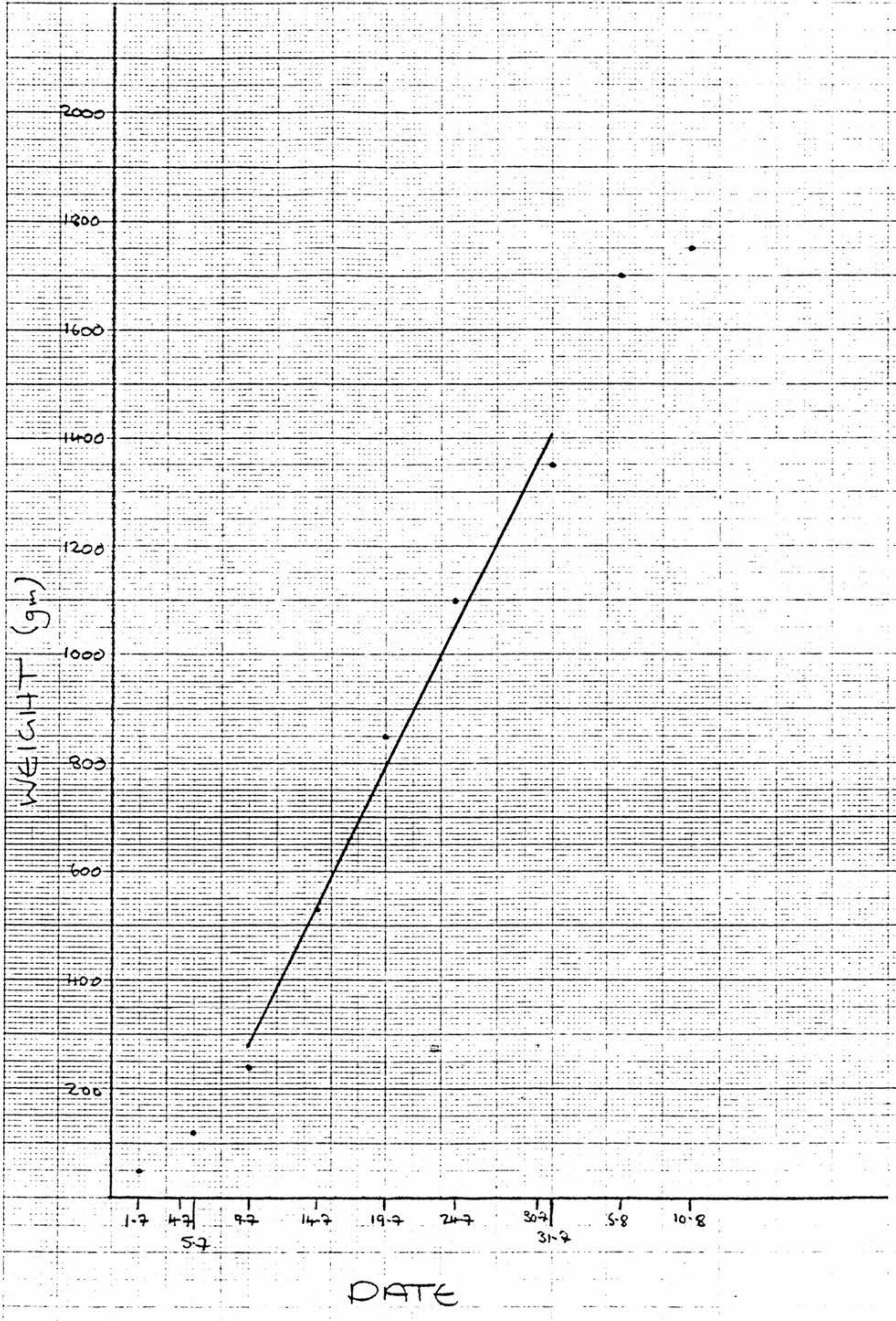
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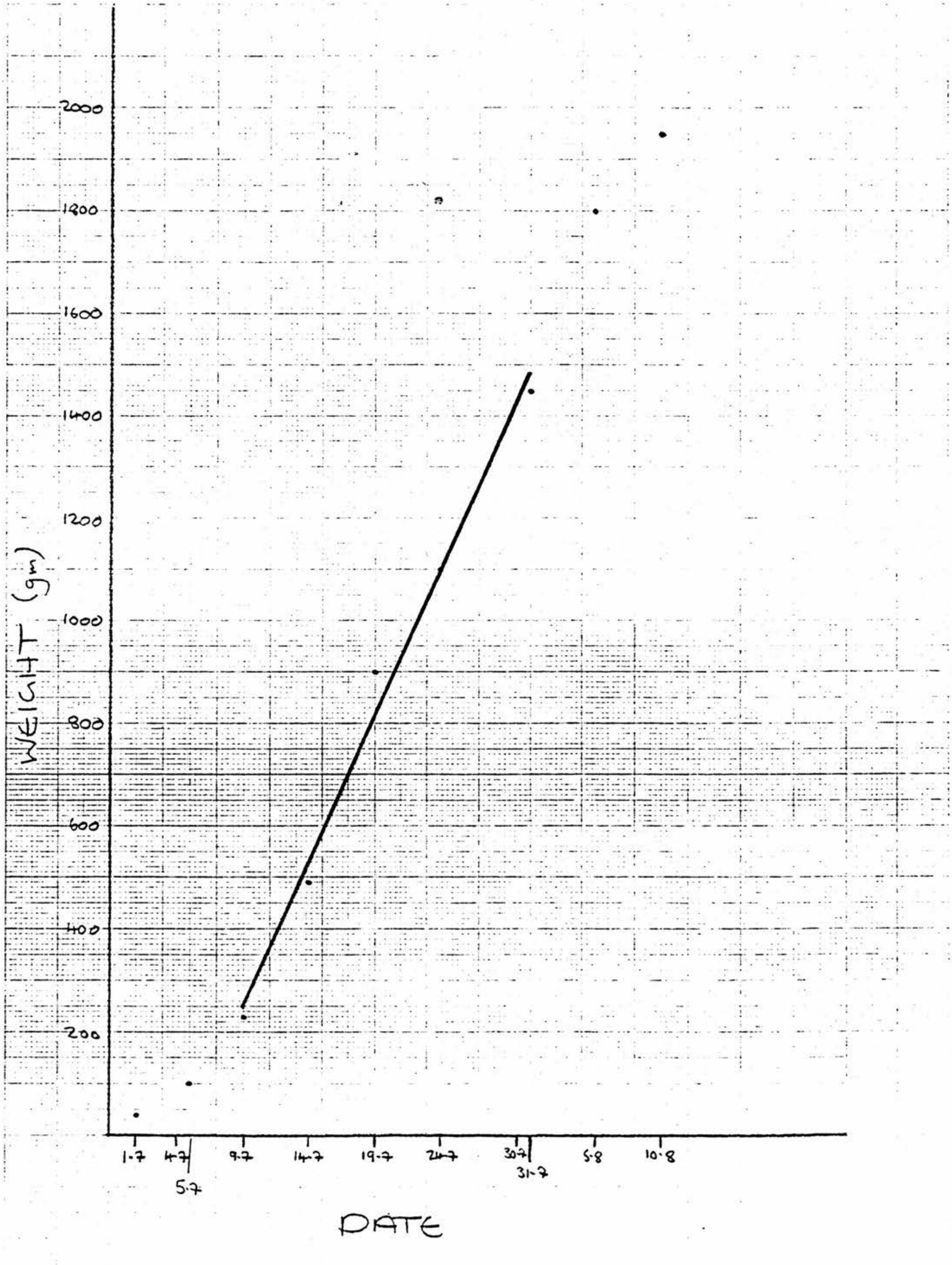

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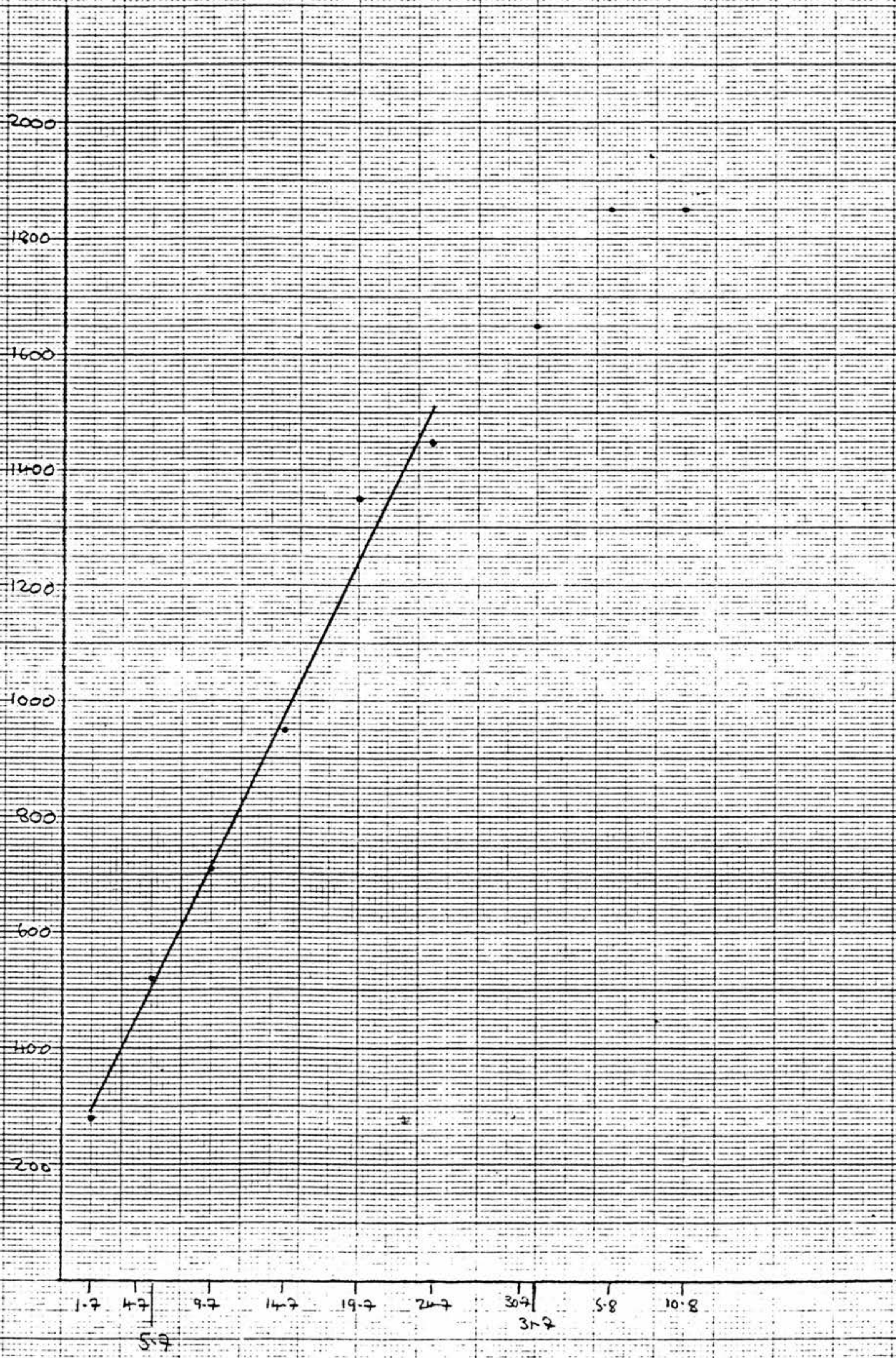
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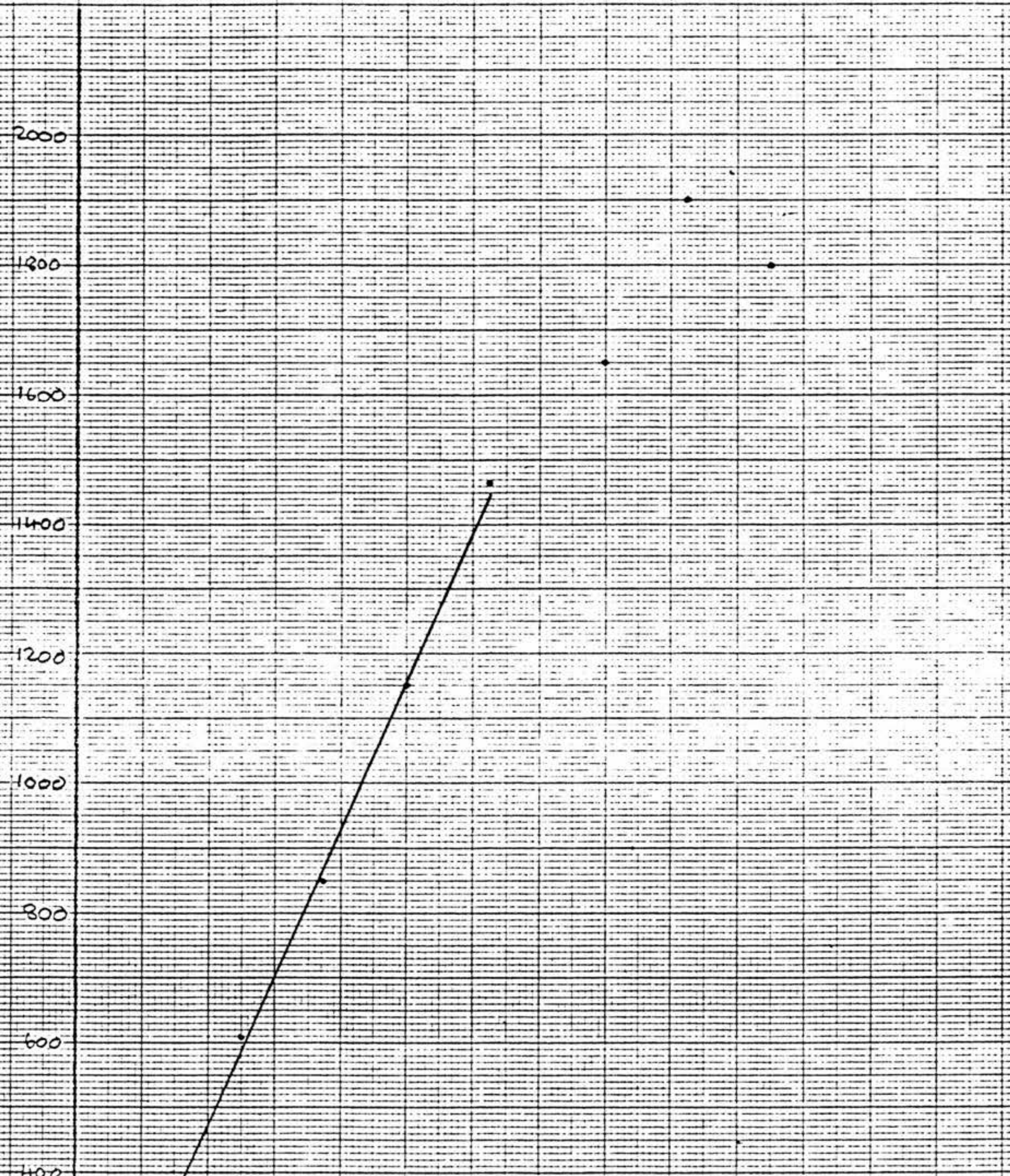
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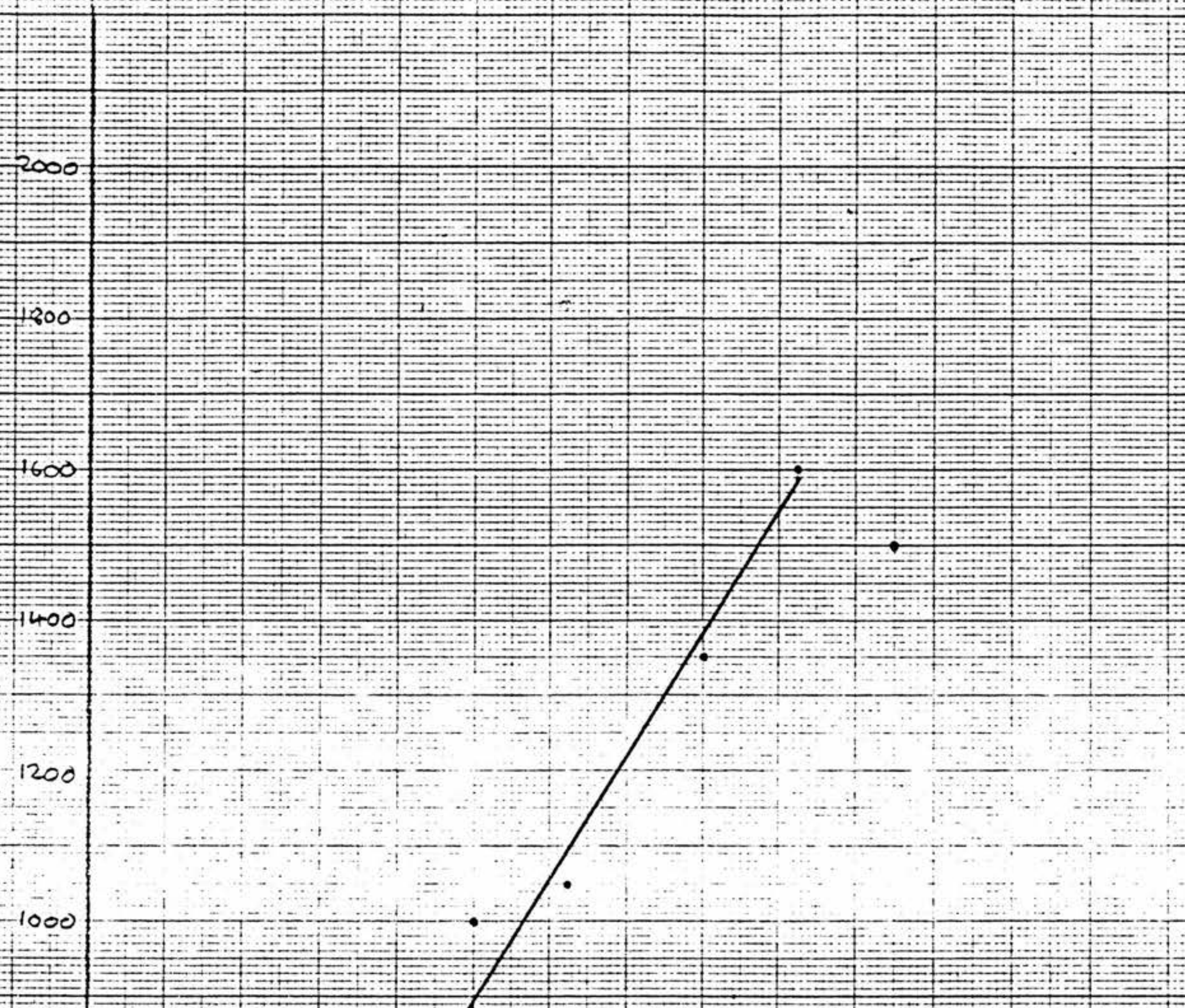
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APPENDIX D.

Return-feed intervals for the 5 pairs observed during the two all-day watches. These are the figures from which the return-feed intervals given in the text were calculated.

Males

Nest number	28.7.86	4.8.86
2	46.5	2.0
3	0.0	72.0
11	52.5	29.0
bel11a	7.0	3.5
22	7.0	1.5

Females

Nest number	28.7.86	4.8.86
2	4.0	8.0
3	9.0	57.0
11	1.0	1.0
bel11a	10.0	16.0
22	5.5	32.0

SUMMARY

Monitoring Methods

1. A single count of nests in early June is often used as an index of the size of the breeding population. This timing is based on the work of Potts (1969). The aim of this study was to confirm that this is the best time to make a count.

2. A part of the study area, with 290 nest sites, was photographed in early April, 1986. Between 12 May and 27 July, nests were checked weekly, and their positions marked on the photographs. Nests were categorised as active, full, half-built or trace.

3. These nests were counted weekly by two independent workers, who simulated a census count. These counts were then compared with the accurate records made using the photographs.

4. There was good agreement between the counts of nests and the checks using photographs for active and full nests. The mean difference between the counts derived from the two methods was only 1.4%.

5. Agreement was also good between the two independent counts of active nests; the mean difference between observers was 2.3%. The difference between counts of half-built and trace nests was 15%, probably due to the difficulties involved in identifying nests at these stages. Overall, the difference in total nest counts was 3.2%.

6. 290 different nest sites were used during the period covered. Of these, 30 sites were used on more than one occasion. The maximum number of nest-sites being occupied simultaneously was 240, on 5 June. The highest count of nests was 237, on the same day.

7. The evidence from this study confirmed that early June was the best time to make a count, though the accuracy of the count is unknown. Care must be taken in generalising from this result: in a very late breeding season, there can be no guarantee that the early June is the best time to count; and in other areas, such as the southwest, where Shags breed earlier than in the northeast, it may be better to count earlier.

8. Occasionally, large numbers of Shags fail to breed, in which case any nest count is likely to be misleading. Thus, any count should include an objective assessment of whether there seem to be fewer nests than might be expected from the numbers of adults present.

Feeding Behaviour

9. The feeding behaviour of seabirds is a topic of importance because they often stand at the top of the food chain, and can be a sensitive indicator of changes in the sea. This study presents data on the feeding behaviour of the Shag under favourable conditions.

10. A total of 71 hours of observational data was collected, made up of two all-day watches, and two three-day series of staggered watches which covered the period from dawn to dusk. The watches were spaced out in such a way as to separate out tidal and diurnal factors.

11. Growth data were taken from 57 chicks from 26 nests in an area distinct from the area which was used for observations.

12. Shags left the island to feed after sunrise, the earliest departure being 28 minutes after sunrise. The mean length of absence was 30.0 minutes, which allowed a maximum feeding range of 7.5 miles, assuming a flight speed of 30 mph (Pearson, 1968). This is enough to allow Shags to fish along the Fife coast.
13. No relationship was found between the tide cycle, and the timing of the feeding of chicks. This seemed to depend on time of day, with

the number of feeds given rising to a maximum value about 3.5 hours after sunrise, and remaining at that level until about 1 hour before sunset. Chicks often were forced to wait before being fed by an incoming adult, for periods of up to 72 minutes. The mean interval between an adult coming in to the nest, and feeding a chick was 22.1 (sd 26.2) minutes for males, and 14.4 (sd 17.5) minutes for females.

14. There was no significant difference between brood size and the number of feeds given to the brood, nor was there any significant difference in growth rates. In the case of feeding rates, larger samp le sizes might have made the result clearer.

Diet

15. The diet of Shags was examined, based on the analysis of pellets, which were easily collected in large numbers from the breeding areas. In addition, regurgitates, which were collected opportunistically while handling chicks, were examined.

16. Regurgitates from chicks were weighed and the constituent fish measured, as soon as possible after collection. Pellets were analysed by dissolving the mucous using sodium hydroxide and then counting the otoliths they contained.

17. The mean weight of regurgitates was 48.7g (sd 28.4) in 1985, and 44.0g (sd 34.0) in 1986. All regurgitates were made up entirely of sandeels, except for one which contained a dragonet (*Callionymus lyra*) and one which contained an unidentifiable fish.

18. The otoliths extracted from pellets were made up of between 88.9% and 99.6% sandeel otoliths by number. Small numbers of otoliths from a number of other species were also found, along with crustacean remains.

19. These results suggest that throughout the year, sandeels are an important prey species for the Shag, though a variety of other prey species are taken. The data do not support a quantitative analysis of diet composition.

Time budget

20. The time budget of the Shag at the nest site was estimated. This forms the first step towards the production of a detailed picture of the activity pattern of the Shag.

21. Observations were recorded throughout the breeding season, during a series of staggered watches which covered the period dawn to dusk over 2 or 3 days. The activities of focal birds were recorded on a checksheet every 30 seconds.

22. The breeding season was divided into 3 stages for the purposes of analysis: the incubation stage, the brood stage, and the post-brood stage. Data were taken for each stage from 7 nests.

23. Both the male and the female spent the same amount of time at the nest throughout the breeding season, although the male spent progressively less time alone on the site, and more time there together with the female.

24. Twenty four categories of behaviour were used on the time budget checksheet, of which 6 accounted for between 95.7% and 98.8% of the time budget. These were: time absent from the nest, preen self, rest, stand, preen chick and sleep.

25. There were no sex differences for any of the 6 major categories of activity. All of the categories except "time absent" showed differences between breeding stages.

26. The use of time budgets as a basis for the estimation of energy budgets was discussed. Comparison of estimates based on time budgets with those derived from the use of doubly labelled water suggests that the accuracy of the time budget technique is doubtful. The doubly labelled water technique has been estimated as being accurate to within 5% (Speakman and Racey, in press). Particularly in the case of large seabirds, there is insufficient data on the energy costs of specific activities to justify the productions of energy budgets based on time budgets.

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