

**Warren Use in Open and Covered Habitats: the
importance of predation for the European
rabbit (*Oryctolagus cuniculus*)**

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Warren Use in Open and Covered Habitats: the importance of predation for the European rabbit (*Oryctolagus cuniculus*)

ABSTRACT

European rabbit (*Oryctolagus cuniculus*) densities, burrow distributions and burrow frequencies were studied in southern Portugal in two types of habitat classes: open and covered habitats. The linear correlation found between rabbit densities and burrow frequencies in open areas suggests that burrows enable rabbits to utilise refugia-free environments such as open grasslands. In addition, by analysing warren sizes it was discovered that group living is only common in exposed areas. The overall conclusions of this study contradict the general view of the European rabbit as being a social species, indicating that group living in the rabbit is the outcome of nest aggregation, which in turn is the result of predation pressure inhibiting colonisation of new locations. These findings have implications for future rabbit management in that targeting large warrens will only be effective at controlling rabbit numbers in open grasslands, a habitat where rabbits extensively utilise burrows and tend to live in aggregated colonies.

1 INTRODUCTION

1.1 The European rabbit: background and biology

Originally from the Iberian Peninsula (Thompson & King, 1994), and first discovered by the Phoenicians in about 5000 B.C. (Rogers & Myers, 1979), the European rabbit (*Oryctolagus cuniculus*) has now colonized, with the aid of human transportation, a vast number of countries worldwide. A keystone species in its native countries it also claims pest status as a result of its robust disposition to eradication and its explosive reproductive capacity. Along with its importance as an ecosystem engineer, seed disperser and valuable food source for many wild animals, the rabbit is appreciated as a game animal, providing the sport with plentiful quarry. This conflicting role means that *Oryctolagus cuniculus* enjoys appreciation and abhorrence simultaneously within many countries.

Mortality rates vary greatly between locations, seasons and years, with deaths resulting from predation, hunting, disease (mainly myxomatosis and viral haemorrhagic disease), drowning and injury. Rabbits have a wide diversity of predators, with seventeen different species of mammals and nineteen species of birds known to regularly prey upon rabbits in southern Spain (Rogers et al., 1994). In the Doñana National Park in Spain a recent study showed that birds of prey account for half the rabbit predation (Moreno, Villafuerte & Delibes, 1996) whilst in France and Great Britain foxes (*Vulpes vulpes*) are probably the chief predators. Unsurprisingly, predator avoidance behaviour is an inherited trait in the European rabbit (Pongracz & Altbaecker, 2000). Myxomatosis (a viral disease transmitted by fleas and mosquitoes) has greatly affected mortality patterns of rabbits since it was first introduced near Paris in 1952. The disease shows seasonal trends, with patterns differing between countries and years. Although this disease still has the potential to kill as many as eighty-three percent of all rabbits in a region, immunity is becoming gradually more common (Rogers et al., 1994). During the first outbreak in Great Britain it killed 99% of all rabbits. Viral haemorrhagic disease arrived in Spain in 1989, and although not as virulent as myxomatosis, has wiped out many local populations in northern Spain (Calvete et al., 1997). This has become of great concern in hunting areas.

Much research has been conducted on the diets of rabbits, resulting in the agreed finding that both grasses and forbs constitute the majority of the rabbits diet. Their diet also shifts with the changing seasons and with the environment they inhabit (Rogers et al., 1994), as would be expected of any environmentally tolerant species. Research in the Doñana National Park in Spain has produced evidence that a rabbit's diet is based more on what food is available following grazing by larger herbivores than on any particular preference (Rogers et al., 1994). Nevertheless the rabbit still requires high quality forage for growth and reproduction. Thus, climate exhibits a strong constraint on rabbit populations by directly affecting the quality of food available. Drought takes many lives, possibly due to the lack of surface water but more likely as a result of failed germinations and reduced plant growth (Myers & Parker, 1975). Terrain is another key constraint because, although rabbits are known to be capable of living above ground, they can only flourish on land where burrows can be built or where there is another form of sturdy cover (Rogers et al., 1994). Predation, the third natural control keeping rabbit populations in check, could perhaps be deemed the most vital one as it is the absence of this restraint that has led to the rabbit gaining a pest status in so many countries. This is depicted best by the example of Australia, where the infamous lack of large carnivores has overridden the impacts of a harsh climate, inferior terrain and virulent disease.

1.2 Rabbit behaviour and ecology

Rabbits are not confined to one particular habitat, living within habitats as diverse as moorland, forests and wetlands; however they show preferences for coastal sand dunes, agricultural pastures and dry heaths (Hulbert et al., 1996; Rogers & Myers, 1979; Myers, Parker & Dunsmore, 1975). Patchy distributions of rabbits are common because of their particular habitat requirements. They generally need ground in which they can dig, suitable forage and adequate ground cover. Rabbits can utilise grasslands as well as areas with scrub (Wheeler, King & Robinson, 1981). Both habitats have their advantages, with scrub providing abundant cover for escape from predators, whilst grasslands possess nutrient-rich forage (Rogers & Myers, 1979). It has been revealed in both Spain and Scotland that rabbits tend to use open areas significantly more than areas with cover (as measured by rabbit pellet densities; Palomares & Delibes, 1994; Hulbert et al., 1996). This opposes the previous belief that the presence of abundant predators causes rabbits to keep close to cover and

consequently forsake the nutritiously-superior grasses (Jaksic & Soriguer, 1981). Numerous studies have revealed that predator risk increases with distance from cover, and that animals often make trade-offs in terms of energy costs and food quality in response to this danger (Hughes & Ward, 1993; Lima, Valone & Caraco, 1985; Ebensperger & Wallem, 2002). However, it seems that by building warrens on land with minimal vegetation rabbits are able to utilise areas away from natural cover (Palomares & Delibes, 1994).

There is a daily pattern to habitat use in that open areas are utilised significantly more during the night whilst in the day rabbits stay close to cover. This behaviour could be an adaptation to changes in predation risk throughout the day, with aerial predators being a major risk only in the daylight, and carnivores (which tend to be nocturnal and rely on ambushing with the aid of cover) being the key threat during the night (Moreno, et al., 1996). As well as highlighting the fact that ground cover is not necessarily danger free, this study emphasises how much the rabbit's behaviour is controlled by predation risk. In western Australia, for example, rabbits regularly occupy the scrub, and such areas are used frequently as refuges (Wheeler et al., 1981). It seems possible that Australia's deficiency in terrestrial carnivores (having only three mammalian species of predators; Myers et al., 1994) means that the nocturnal danger is much reduced, consequently allowing rabbits to utilise cover to a greater extent.

There is a dominance hierarchy amongst rabbit populations with experiments on captive rabbits revealing that males (bucks) will fight for dominance and the winner will claim the loser's burrow and mate (Mykytowycz, 1958). Bucks will only desert their mates due to displacement by a more dominant buck or by advancement to a larger warren (Mykytowycz & Gambale, 1965) and bucks will always defend their females and their burrows if possible (Lockley, 1964). When the mating season arrives territoriality becomes more aggressive and male rabbits mark out individual territories, which they subsequently defend throughout the season. The dominant female (doe) also displays elevated levels of aggression towards subordinates and when defending its territory (Mykytowycz, 1958). Even during this time, though, it is not uncommon for two bucks to inhabit the same warren together, albeit in separate sections, indicating that rabbits can tolerate each others presence. Such tolerance is

also found with their young, with weaned kittens remaining in their parents' burrows up until the next breeding season (Lockley, 1964). Second-ranking does are also allowed to share the dominant male's burrow alongside the more aggressive matriarch, revealing that polygamy is an accepted occurrence (Mykytowycz, 1958).

Dispersal in *O. cuniculus* is male biased, however females often leave their natal burrows also. Natal dispersal occurs during the first five months of birth, with normally more than 50% of all juveniles leaving their burrows. It is common for all males to disperse, often moving up to seventy metres away from their birthplace (Künkele & von Holst, 1996). A significantly lower proportion of females disperse, and when they do they move much shorter distances. Female dispersal seems to be inversely density-dependent, and it has been found that during periods of high rabbit densities philopatric females produce significantly more offspring than females that have dispersed (Künkele & von Holst, 1996), indicating that the choice to remain in the natal burrow during such conditions is beneficial.

1.3 The importance of warrens

The majority of rabbits live in burrows that they have dug out of the ground. In fact it is this behaviour that earned the rabbit its scientific name, *Oryctolagus*, meaning 'digging hare' (Thompson & King, 1994). A network of burrows is termed a warren. A deep depth of light soil on a sloping site are preferable components of burrow building ground (Mykytowycz & Gambale, 1965). It is often stated that sandy ridges are necessary for burrow construction (Rogers & Myers, 1979), however this is not a vital feature (personal observation). An elevated position seems to confer an advantage to the inhabitants, possibly because it reduces the risk of flooding (Myers et al., 1975). Female rabbits do the majority of the digging within the warrens (Myers & Poole, 1961; Lockley, 1964) and once they have given birth to their first litter they tend to remain with that warren for the rest of their lives. It is known that females compete for vacant breeding sites, with the larger warrens being the most sought after (Cowan, 1987). During the breeding season subordinate does dig short burrows, unconnected to other burrow networks and constructed solely for raising litters in, which are known as 'stops' (Mykytowycz & Gambale, 1965). In fact it seems that a lack of nest sights is a major restriction to the number of young that can be produced, making large warrens a valuable asset.

However, some populations of rabbits do not build warrens and instead live above ground, using shrubs as hiding places when threatened (Wheeler et al., 1981). This behaviour has been blamed for the failure of gassing in controlling rabbit numbers (Kolb, 1991). Although it was at first thought to be a behaviour only conducted by subordinate rabbits it is now believed that it could be an inherited trait that is becoming more common due to natural selection driven by myxomatosis (Kolb, 1991). Rabbits are more susceptible to viruses when living in confined quarters such as burrows, and so disease could be promoting the survival of surface-dwelling rabbits. However, there are substantial reports of surface living in rabbits prior to the existence of myxomatosis (Kolb, 1991). Another possibility is that living on the surface is a natural habit for rabbits to do but is not always possible due to a lack of suitable habitat (i.e. sufficient ground cover). A detailed study in Australia revealed that the majority of rabbits lived above ground even though there were many available burrows and the ground was suitable for digging (Wheeler et al. 1981). Additionally, in England rabbits were found to only live permanently in warrens in the middle of fields (i.e. exposed areas) and although there were burrows available at the forest edge rabbits were found most often above ground hiding within vegetation (Kolb, 1991). Such evidence indicates that there are hidden benefits to life above ground.

An objective of this project was to determine the importance of warrens by testing a prediction made by Palomares and Delibes (1997) that burrows are necessary for rabbits to utilise exposed land, however in covered areas they are of less value as shrubs provide alternative refugia from predators. If this prediction is true then there would be a positive association between rabbit burrow entrances and rabbit densities in areas of low ground cover but no such relationship in areas where there is substantial cover for rabbits. This has been shown previously by Palomares and Delibes (1997) in the Doñana National Park, however other studies are yet to verify this finding. To extend the work of Palomares and Delibes (1997) a further aim was to test for a relationship between burrow densities and ground cover. It was theorised that the more cover there is then the less rabbits would rely on burrows (as seen by a reduced abundance of burrows).

1.4 Group living in the European rabbit

It has been said that rabbits are gregarious by nature and are ‘drawn towards the bustling centre warren’ (Lockley, 1964). However, research by Cowan (1987) has suggested that group living in rabbits has evolved via the competitive route rather than the co-operative route. The finding that group living acquires rabbits no net benefits (as seen by a reduction in lifetime reproductive success in larger group sizes) led Cowan to the notion that aggregations of rabbit are simply the product of patchily distributed nest sites rather than sociability. This idea is supported by a study showing that rabbits display higher vigilance in larger feeding groups (Roberts, 1988). The outcome of such behaviour is costly as less time is available for feeding. Other studies on cooperative groups of animals, such as groups of kangaroos and flocks of birds, have contradictory findings. They have found that individual vigilance reduces with increasing group size, as predicted by the ‘selfish herd’ theory (where individuals locate themselves within the group so that they are less at risk from predation; Hamilton, 1971) and the ‘many eyes’ hypothesis (when groups are more likely to spot danger than one lone individual is; Scheel, 1993; Roberts, 1988; Jarman, 1987; Krause & Ruxton, 2002). However investigations into vigilance in naturally solitary animals support Roberts’ findings, with solitary species being comparatively more vigilant than gregarious species (Tchabovsky, Popov & Krasnov, 2001), and when in groups they increase their vigilance rather than conforming to the ‘group size effect’ hypothesis (Monaghan & Metcalfe, 1985).

Other costs generally associated with group living include competition for food, increased visibility to predators and increased risk of disease (Ebensperger & Wallem, 2001; Hoogland, 1981). Rabbits have been found to be susceptible to all these factors, which is illustrated in females’ anti-social behaviour to unrelated juveniles and other females (Cowan, 1987). This is not to say that rabbits receive no benefits to group living. Alarm calls may exist between rabbits (although literature is inconsistent on this matter; Roberts, 1988; Lockley, 1964), and there could be thermoregulatory benefits (Ebensperger & Wallem, 2002). It is also likely that there is a degree of lowered predation risk as a result of the ‘dilution effect’ (the larger the group the less chance each individual has of being caught) and the ‘confusion effect’ (where predators find it difficult to single out an individual from a group) (Krause & Ruxton, 2002; Inman & Krebs, 1987).

In response to the contradictory opinions concerning the gregariousness of rabbits a further aim of this study was to determine whether group living was more common in open areas (where such a social structure could have beneficial impacts on predator avoidance) than in covered areas. Additionally, it was questioned whether exposed areas, on average, contained larger groups of rabbits (as measured by number of entrances per warren; Myers et al. 1975; Myers & Parker, 1975) than covered sites did. Such data would provide additional information on the nature of group living in rabbits and thus help determine the evolutionary process that has led to this form of existence.

1.5 Burrow measurements

Four different measures of burrow densities were used to provide guidance as to the most valuable method for future research. The different measurements were: one measurement of all burrows discovered, one of only active burrows located, one of all warren entrances discovered, and one of all active warren entrances found. The objective was to determine whether one measurement proved superior to the others in terms of correlating with pellet densities.

2 STUDY AREA AND METHODOLOGY

2.1 Study area

Data was obtained at 16 sites in central Alentejo, Portugal, in the Monseraz locale during June and July 2003. Many of the study sites were located near to the newly formed Alqueva reservoir (appendix 1). This reservoir is a result of the Alqueva dam construction project, which was completed in 2001 along the Guadiana River. In preparation for the immense flooding, up to 20,000 hectares of land were cleared of scrub and trees in the immediate vicinity of the river (GEOTA, 2003). This subsequently produced unusually large areas of open grassland bordering the expanding Guadiana River. The drastic operation has removed habitat that rare and endangered flora and fauna rely upon. The critically endangered Iberian Lynx (*Lynx pardinus*) and the Imperial eagle (*Aquila heliaca*) are two species whose future will undoubtedly be compromised by the controversial flooding (Duerr, 2002).

The Alentejo region is dominated by montado landscape, which is defined as open oak woodland, namely cork oak (*Quercus suber*) and holm oak (*Quercus ilex* & *Quercus rotundifolia*). Farming of grazing animals is a major industry in Alentejo, and because montado is semi-natural (being maintained by grazers), cattle, sheep and goats are important members of the ecosystem (Duerr, 2002). The region is also used to grow crops and cork oak trees - Portugal is the world's largest cork supplier.

In the study site this habitat was interspersed by grasslands (Baptista & Fernandes, 2003) and cistus (*Cistus ladanifer*) dominated ground (personal observation, 2003). It is representative of many mediterranean environments and accordingly has a semi-arid climate, with cool wet winters and hot dry summers. During the study period there was less than 50mm of rainfall and temperatures ranged from 12°C to 41°C with an average daily temperature of 29°C.

2.2 Field sites

Sixteen sites were studied in total, and were categorised into either 'covered' or 'open' sites. 'Covered' referred to land that had more than 30% of its surface covered by shrubs, trees or rocks. 'Open' sites had less than 30% cover. Equal numbers of open and covered sites were investigated. Sites were chosen primarily by their habitat

(ground vegetation was too dense in some areas to conduct pellets counts accurately), their accessibility and their apparent rabbit densities - only locations with noticeable rabbit populations were included. All sites were deemed to possess typical Alentejo habitat, which is generally considered to be montado, open grassland or cistus. All of the sites were on land officially designated as hunting ground. It was not possible to measure the area of the sites as they were often part of a continuous heterogeneous landscape with no clear boundaries. However, all sites were at least 300m² so as ensure that all data would be free from edge effects.

The multipurpose landscape that covered the study region provided diverse habitats to work in, whilst the clearing that had been undertaken had resulted in the region possessing an unusually large number of grasslands, scattered with clumps of boulders and their associated thickets and trees. This was optimum rabbit habitat, containing abundant forage along with some cover. Such areas were selected as locales for the open sites. Consequently most of the open sites were dominated by grassland, all with a small number of cork oaks, thickets and /or piles of boulders. Details of sites can be found in table 1. Typical shrub families found within the study sites included *Leguminaceae* and *Ericaceae*. Within the tree dominated covered sites, small natural clearings were common. Photographs of all the sites were taken and these were analysed by two other individuals to help assign an unbiased rank to each site. The rank represented relative overall ground cover for each site (table 1).

2.3 Transects

Three 100 metres strip transects were conducted at each site (Greenwood, 1996). These transects ran parallel to one another and were separated from each other by a distance of 40 metres. They were situated across the approximate centre of each site, thus preventing edge effects. A compass was used to ensure that the transects were conducted in a straight line.

2.3.1 Faecal pellet counts

Rabbit pellets were counted in each site to provide a relative estimation of rabbit densities. Pellet counting is a widely used method for estimating lagomorph densities (Murray et al., 2002; Kolb, 1991; Hulbert et al., 1996), and this study involved an uncontrolled census (Macdonald, Mace & Rushton, 1998; Sugimara et al., 2000),

where each site was visited just once. Due to the slow decay rate of faecal droppings (one study has shown that complete decay in an environment comparable to southern Portugal will take three years and nine months – Petterson, 2001) uncontrolled sampling collects data on rabbit densities from the past year, or more, rather than estimating current rabbit densities. However, this methodology was considered the most practical and appropriate, as it allowed large amounts of data to be collected in minimal time and provided data that could be utilised comparatively, which was sufficient for this investigation.

Pellets were counted in four quadrats along each transect, with 12 quadrats being conducted per site. One quadrat was done within every 25 metre length of the 100 metre transect, however exact locations were randomly assigned. Within each quadrat pellets were only counted in the four corner subsections measuring 33cm² to minimise searching time. Only intact pellets were considered.

Site	Dominant habitat	Cover rank
Open 1	Grassland and oak trees	5
Open 2	Bare ground, grassland & shrubs	2
Open 3	Grassland	3
Open 4	Long grassland	4
Open 5	Scrub, rocks and grasses	8
Open 6	Boulders & grassland	6
Open 7	Boulders & grassland	7
Open 8	Sparse grassland	1
Covered 1	Shrubs and trees	13
Covered 2	Thickets & trees	15
Covered 3	Grassland & trees	11
Covered 4	Grassland & trees	10
Covered 5	Bushes & trees	14
Covered 6	Boulders & trees	12
Covered 7	Long grassland & dispersed trees	9
Covered 8	Cistus	16

Table 1 Site information

2.3.2 Burrow counts

Burrows were searched for along each transect and within a five metre radius around the transect line. Thus in each site a total of 3300m² of ground was intensely explored. It was noted whether the burrows were in present use (active burrows) or had not been used for some time (disused burrows; Myers & Parker, 1975). This was deduced by the state of their entrances: the presence of droppings at the entrance and evidence of cleared soil was an indication of activity. More precise methods could have been used to confirm that the burrows were being currently used, however it was thought that this would give too detailed results. As already stated, rabbit droppings take years to decay completely, and presumably intact pellets can be at least a year old. Thus it would not be sensible to use a measurement for accumulative rabbit densities from the past year whilst using burrow counts representing burrows used only by the current population.

Burrows grouped closely together were identified as entrances to a warren, thus the number of such entrances at every warren was noted. This data would subsequently provide information on the relative number of rabbits living within the warrens as the number of entrances into a warren is closely related to the number of nest sites within it (Myers et al., 1975, Cowan, 1987). Additional information concerning the microhabitat and geographical situation of the warren or isolated burrow was also gathered.

2.4 Data analysis

All data was compiled into an Excel spreadsheet and SPSS was used to statistically analyse the information. The data was divided into three sections: data obtained from open sites, data from covered sites, and all data. Burrow information was separated into active and all (total) burrows found, all warren entrances and only active warren entrances. Only groups of three or more burrows were classed as warren entrances (as a warren was defined as having a minimum of three entrances). It was presumed that the warren entrance data would be more reliable than data incorporating lone burrow frequencies. This is because warrens are much more visible than single burrows are – the chance of missing isolated burrows was deemed much higher than that for grouped burrows.

2.4.1 *Warren entrances in open sites*

To test for an association between burrow numbers and rabbit densities in open sites, the parametric Pearson's product-moment correlation was performed on the pellet counts from the open sites and the burrow information from the open sites (the Kolmogorov-Smirnov test revealed a normal distribution whilst a scatter graph showed no outliers). Four tests were performed: to assess the relationship between pellet numbers and active warren entrances, pellet numbers and total warren entrances, pellet numbers and active burrow entrances, and finally pellet counts and total burrow entrances.

2.4.2 *Warren entrances in covered sites*

The Kolmogorov-Smirnov test showed the data was normally distributed and no outliers were apparent on the scatter graph. Consequently the same statistical tests were conducted as explained above, however only data from the covered sites was used.

2.4.3 *The relationship between burrows and cover*

As previously described, every site was given a cover ranking that directly related to the perceived amount of shrub, rock and tree cover each site had in comparison to all the other sites. Consequently the data had to be analysed using a non-parametric tool. A regression was desired because a cause and effect relationship was under enquiry. However the only non-parametric regression test is Kendall's robust line-fit method (Dytham, 1999), which is not supported by any statistical package and is thus time consuming and error-prone. The alternative, which is generally understood as an acceptable substitute, is the Spearman's rank-order correlation. This is the statistical test that was used.

The relationship between relative amount of cover and burrow frequencies was tested. However, rabbit densities had to be taken into consideration as these were likely to influence burrow density. Therefore the average number of burrows per hundred pellets was used instead. Two tests were performed using the warren entrance data: one on only active warren entrances and one on all entrances discovered, whilst two tests were run on the complete burrow data set (all burrows and just active ones).

2.4.4 Group living

To test whether warren use was more common in open areas than in covered areas the number of warren entrances in the two habitat categories were compared using a Mann-Whitney U test. The two sets of data (covered and open sites) proved not to have equal variance and thus a non-parametric test was required. Only data of three or more burrows per warren were used (i.e. only certified warren data). For each site the number of warren entrances was obtained. This value was subsequently modified to give the average number of entrances per 100 pellets. In this way rabbit density was accounted for.

The Mann-Whitney U test was used again to test all the burrow data, not simply the data from just three or more burrows. In other words solitary burrows were included alongside groups of burrows. This test aimed to assess whether rabbits lived in, on average, larger groups in open sites than in covered sites. The average warren size per site was calculated and subsequently divided by the pellet count for that particular site.

3. RESULTS

3.1 Relationship between rabbit densities and burrow numbers

3.1.1 Open sites

The Pearson product-moment correlation indicated a significant positive association between number of pellets and: the number of active warren entrances ($r^2 = 0.933$, d.f. = 6, N = 8, $P < 0.01$), the number of total warren entrances ($r^2 = 0.980$, d.f. = 6, N = 8, $P < 0.01$); the number of active burrow entrances ($r^2 = 0.924$, d.f. = 6, N = 8, $P < 0.01$), and finally the number of total burrow entrances ($r^2 = 0.978$, d.f. = 6, N = 8, $P < 0.01$). See figure 1.

3.1.2 Covered sites

All variables were normally distributed. As predicted, no correlation was evident between pellet frequencies and the number of burrows (figure 2), both active ($r^2 = 0.009$, d.f. = 6, N = 8, $P > 0.05$) and all burrows ($r^2 = 0.175$, d.f. = 6, N = 8, $P > 0.05$); and pellet frequencies and the number of warren entrances, both active ($r^2 = 0.047$, d.f. = 6, N = 8, $P > 0.05$) and total ($r^2 = 0.158$, d.f. = 6, N = 8, $P > 0.05$). However, due to the small sample size, the significance of these findings is questionable.

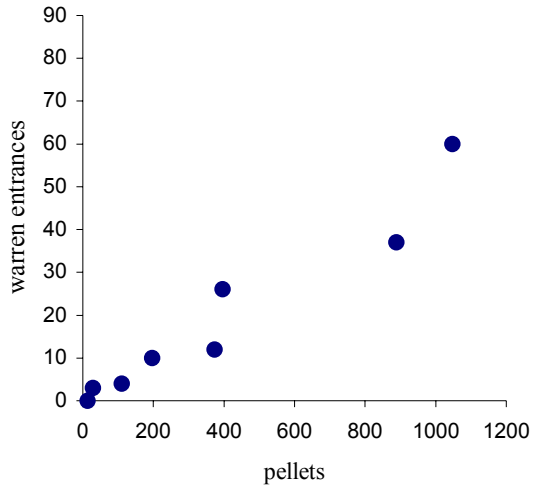
3.2 Effect of cover on burrow frequencies

It was believed that burrows would be less common with more ground cover, and this was verified by applying the Spearman's rank correlation, which revealed a strong negative correlation between amount of cover and burrow counts (figure 3). This was conveyed in every different burrow measurement, with counts of active warren entrances providing the strongest correlation ($r_s = -0.687$, d.f. = 16, N = 16, $P = 0.003$). Results using the measurements of total warren entrances ($r_s = -0.004$, d.f. = 14, N = 16, $P < 0.01$), all active burrows ($r_s = -0.009$, d.f. = 14, N = 16, $P < 0.01$) and all burrows ($r_s = -0.008$, d.f. = 14, N = 16, $P < 0.01$) were also highly significant.

Figure 1. The relationship between rabbit densities (as measured by pellet counts) and the frequency of warren entrances in open sites.

Active warren entrances

$r^2 = 0.933, P < 0.01$



Total warren entrances

$r^2 = 0.980, P < 0.01$

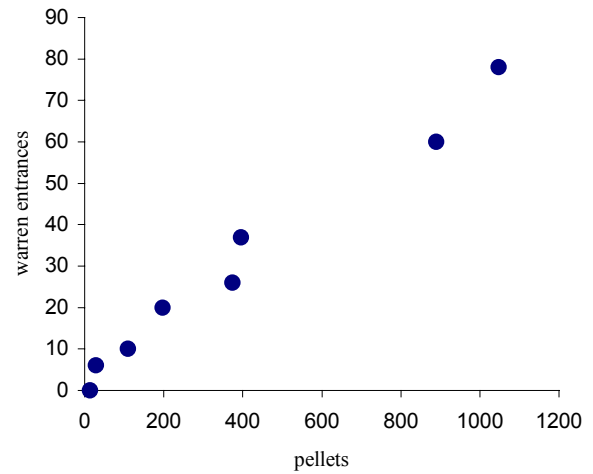
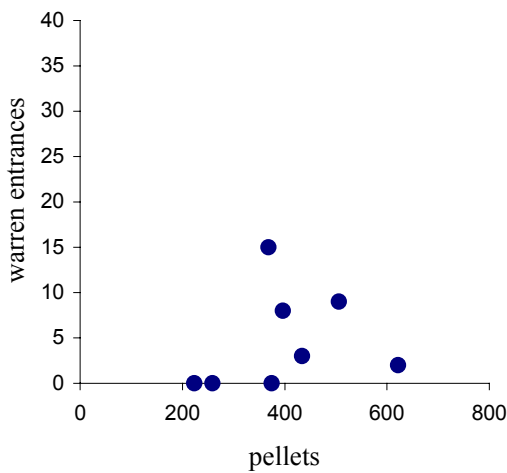


Figure 2. The relationship between rabbit densities (as measured by pellet counts) and frequency of warren entrances in closed sites. The Pearson's correlation consistently shows no significant correlation.

Active warren entrances

$r^2 = 0.047, P > 0.05$



Total warren entrances

$r^2 = 0.158, P > 0.05$

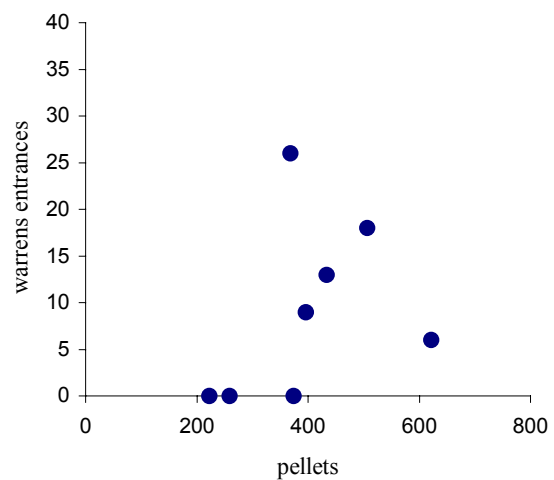
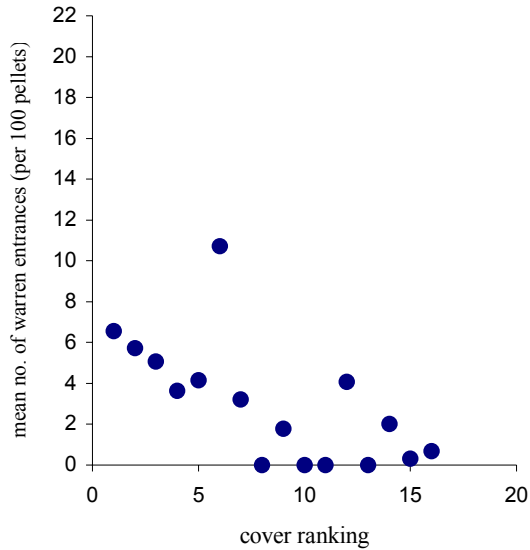


Figure 3. Correlation between a) warren entrances or b) burrow densities and amount of cover. The Spearman’s rank correlation reveals a negative correlation.

a) Warren entrance numbers in relation to cover

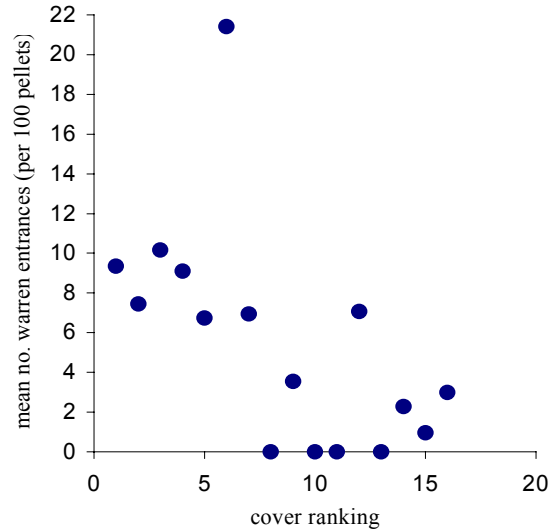
Active warren entrances

$r_s = -0.687, P = 0.003$



Total warren entrances

$r_s = -0.004, P < 0.001$

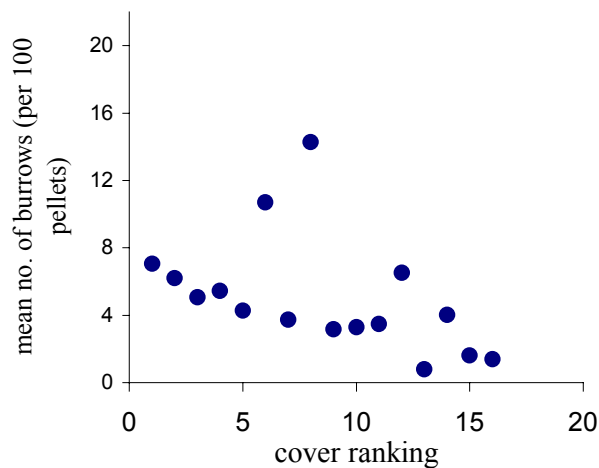


Total warren entrances

b) Burrow numbers in relation to cover

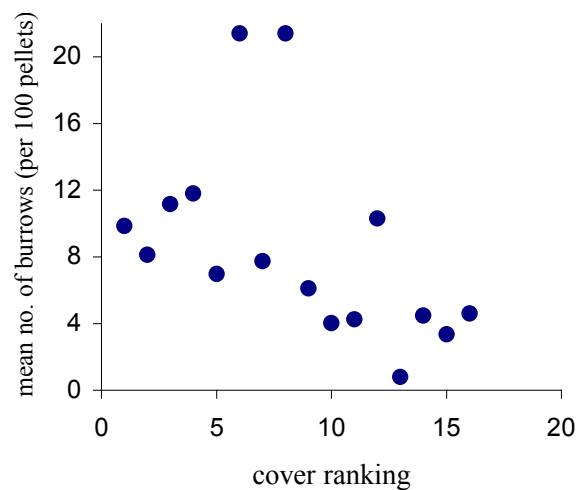
Active warren entrances

$r_s = -0.009, P < 0.01$



Total warren entrances

$r_s = -0.009, P < 0.01$



3.3 Group living

3.3.1 Effect of ground cover on warren size

As predicted, all the large warrens were predominantly confined to the open sites (table 2). In fact although sizeable warrens were discovered in covered areas none had greater than ten entrances (as was often found in open sites). This pattern was verified by the Mann-Whitney U test (the data did not have equal variance), which revealed a significant difference between the average number of warren entrances (per 100 pellets) in open sites and those found in covered sites ($U = 8.5$, $N_{1,2} = 8,8$, $P < 0.05$; figure 4).

Site	Cover rank	Entrances per warren				Total no. warrens
Open 8	1	3	3	6	18	4
Open 2	2	26	48	4		3
Open 3	3	20				1
Open 4	4	11				1
Open 1	5	14	3	43		3
Open 6	6	3	3			2
Open 7	7	20	6			2
Open 5	8					0
Covered 7	9	6	3			2
Covered 4	10					0
Covered 3	11					0
Covered 6	12	9	5	6	6	4
Covered 1	13					0
Covered 5	14	3	6			2
Covered 2	15	3	3			2
Covered 8	16	8	5			2

Table 2 Number of and size of warrens discovered at each site. Note that three is the minimum number of entrances - less than two entrances were not classified as warrens.

3.3.2 Effect of ground cover on solitary burrow frequency

A separate analysis was conducted incorporating all burrow data, rather than simply just data of groups of three or more burrows entrances. Data of solitary burrows was questionable as it was thought that in sites with dense vegetation the likelihood of seeing all lone burrows would be low. However, the results of the Mann-Whitney U test proved highly significant ($U = 0.000$, $N_{1,2} = 8,8$, $P < 0.01$) revealing that covered areas tended to have smaller burrows, and more solitary burrows (see appendix 3), than exposed locations did (figure 5).

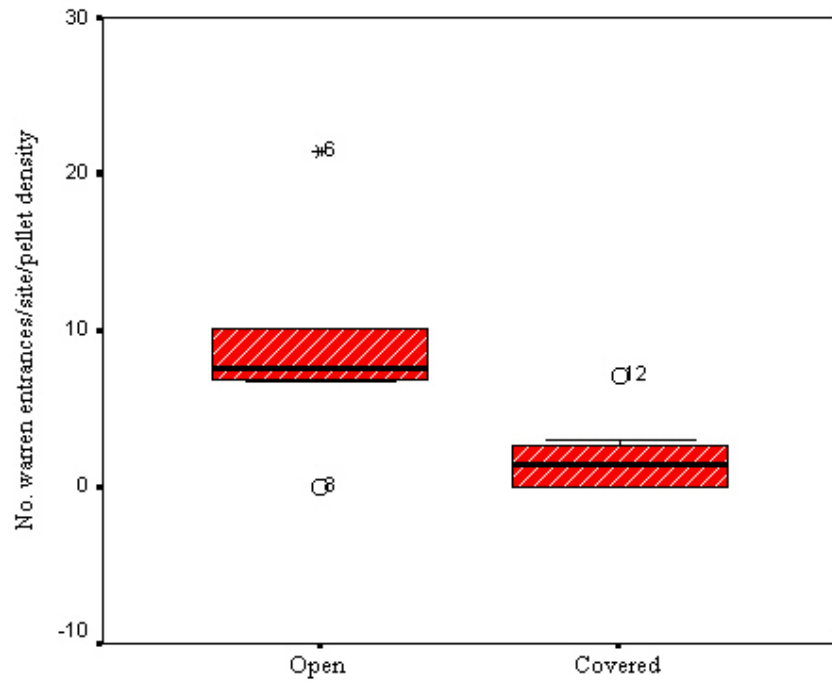


figure 4 A box plot showing the differences between the frequency of warren entrances in open and covered sites. The Mann-Whitney U test statistically verified these differences ($U = 8.5, P < 0.05$).

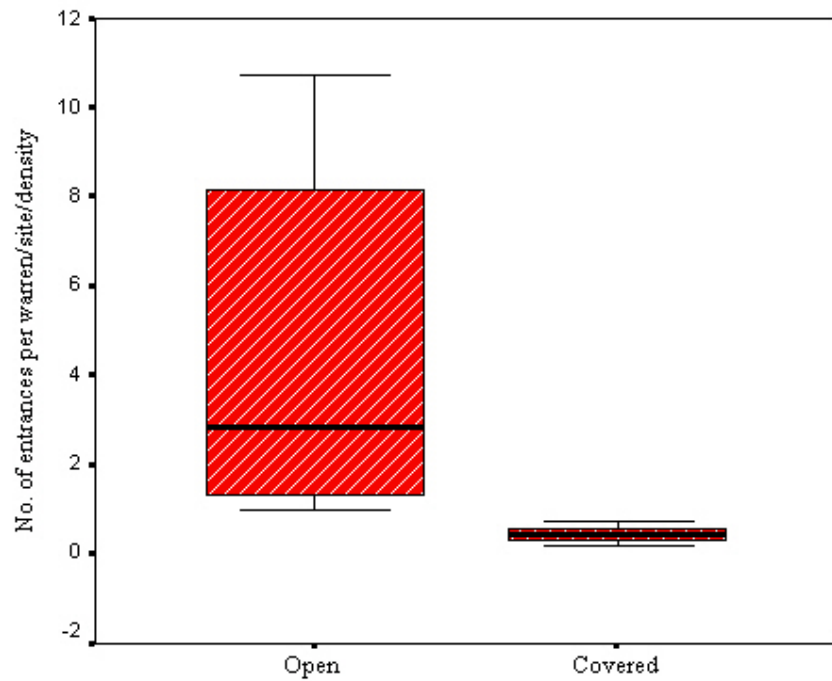


figure 5 Differences in warren sizes between open and covered sites. The Mann-Whitney U test statistically verified these differences ($U = 0.000, P < 0.01$).

4 DISCUSSION

4.1 Methodology

Counts of total warren entrances proved to give the strongest correlation ($r^2 = 0.980$) in the test for the relationship between rabbit densities and burrows (fig. 1). However, counts of active warren entrances provided the strongest association when testing cover rank against burrows ($r_s = -0.687$; fig. 3). Either way it would suggest that collecting warren data is just as good as using all burrow data, and probably better. In addition, it is less prone to error as visibility of warrens is undoubtedly higher than that of solitary burrows, and it is also a more efficient technique because searches can be carried out faster and need not be conducted on foot. Previous rabbit studies have used horseback searches (Rogers & Myers, 1979) that, whilst being inadequate for complete burrow searches, are sufficient for warren searches.

4.2 Warren use

4.2.1 *The importance of burrows*

The findings in this study support those found by Palomares and Delibes (1997) in that there is a positive relationship between warren entrance densities and pellet densities in open areas (figures 1). They also provide compliant detailed information concerning the connection between cover quantity and burrow frequency: in denser cover less burrows are built (figure 3). This infers that warrens are highly important for rabbit existence, but only in exposed locations. In covered areas it is possible that rabbits take advantage of the ground vegetation rather than dig their own burrows, which is energetically expensive and potentially dangerous. However, because burrows were still discovered in covered locations it cannot be said that vegetation is an ample substitute to holes in the ground. As previously explained, mammalian carnivores require cover for ambushing their prey (Moreno et al., 1996), and so it is plausible that burrows still provide distinctive benefits to rabbits even within vegetated areas.

4.2.2 *Group living*

More total warren entrances and on average larger warrens were found in open sites than in covered sites (figures 4 & 5). A similar result was discovered by Wheeler et al. (1981), whose open pasture study site contained multiple warrens, whilst

surrounding patchy vegetation contained very few warrens. This implies that group living is more common in exposed locations than in covered ones. There could be a number of reasons for this disparity. Using the results from this study together with the literature, four possible explanations are discussed below.

Possibility 1: The predatory risk hypothesis

It is a common generalisation that predation threat favours group living (Ebensperger & Wallem, 2002). Thus the rabbit, which forms the staple diet of a wide variety of carnivores and whose mortality rate is high, would likely conform to this belief. The results of a study conducted on degus (*Octodon degus*), a New World burrowing rodent, are similar to those found in this study, in that degus in exposed patches group significantly more than degus in dense microhabitats (Ebensperger & Wallem, 2002). Multiple studies on mammals have found a common pattern of reduced predatory risk for group members as opposed to solitary individuals (Inman & Krebs, 1987), indicating that generally group living mammals conform to the predatory risk hypothesis. Thus, rabbits could be living in groups in an attempt to reduce predation, and thus presumably predation pressure is greater in exposed areas than within cover.

However, evidence suggests that cover is often just as dangerous as open areas (Moreno et al, 1996), with mammalian carnivores hunting within the cover during the night, and birds of prey searching open areas by day. Also, if group living has evolved in rabbits as a method of reducing predation on individuals then the net gains of reduced predation must outweigh any losses that are received as a result of group living. It is also likely that rabbits will have evolved certain social practices that enhance the performance of a group to predator avoidance, behaviours that are common in other mammal species that are known to have evolved into social groups as a way of lowering predation.

Instead, previous research has discovered that rabbits receive no net gains from group living (Cowan, 1987). Cowan found that group productivity was higher in single female groups than in multi-female groups (lone females were three times more successful at breeding than females living amongst other females) and males did not benefit from a larger female to male ratio, as it seems that males cannot monopolise, on average, more than two females. Further more, unlike other social mammals,

rabbits do not display reduced vigilance whilst in groups – a behaviour evolved to take advantage of the ‘many eyes theory’. Roberts (1988) discovered that individual rabbits in larger groups increased their vigilance (and thus had less overall feeding time), indicating that rabbits feel less secure surrounded by non-consort rabbits than they do when alone or accompanied by one mate. Rabbits’ aggressive behaviour supports these conclusions, with grouping of burrows resulting in territorial confrontations amongst males. When individuals are more dispersed such behaviour is less common (Cowan & Garson, 1985).

Other benefits for the rabbit may still be obtained by group living, however, for example increased awareness and selfish herd effects. Rabbits have alarm calls, however it is tenuous as to how valuable these are to other rabbits (Cowan, 1987; Roberts, 1988). It would be interesting to test whether there is a selfish herd effect within rabbit populations, however this is difficult to assess amongst wild populations (Hoogland, 1981). Such advantages would explain the preference for grouping in open areas as opposed to cover, as they are only of assistance in situations when prey can be detected in advance of an attack (Scheel, 1993). An increased number of burrow entrances in which to escape into has also been suggested as an advantage (Hoogland, 1981). However, although burrows are available, it has been observed that when surprised rabbits will generally favour running to vegetative cover rather than into burrows (Wheeler et al., 1981; personal observation), thus this benefit is not exploited by rabbits.

Possibility 2: Social facilitation of activities

It is likely that, as has been found with degus (Ebensperger & Wallem), group warren excavation is more efficient than solitary digging. More soil per individual can be excavated when digging is synchronised and thus deeper, and consequently safer, warrens can be created. Many social species also assist in helping raise young (Krause & Ruxton, 2002), however if this was evolutionary important then there would be increased survival in communal nests, which evidence suggests is not so (Cowan, 1987). The main argument against the theory however is the lack of explanation it offers for the differences discovered between the open and covered habitats.

Possibility 3: Habitat shortage

This study's results are comparable to those discovered by Cowan & Garson (1985) studying rabbit social behaviour in two contrasting habitats: a chalk hill site and a coastal dune site: they too found that different warren sizes were related to different habitats – that smaller warrens were more common in the sand dunes whereas the chalk site supported more complex burrow systems. During their study period burrows were highly clustered at the chalk hill and there was little change in the amount of burrow space available, even though the population fluctuated greatly, whilst on the sand dunes new burrows were easily and often created. A similar pattern has also been found in yellow-bellied marmots (*Marmota flaviventris*) (Armitage, 1962), suggesting that there is a common factor resulting in aggregation whilst simultaneously hindering the creation of new refuges. It seems sensible to speculate that a limitation in the availability of suitable digging habitat could be the probable cause. With insufficient digging ground rabbits (and marmots) would be forced to either forego burrows altogether, extend existing warrens or dig new burrows in the only available good-quality ground, which is likely to already possess a warren, consequently resulting in aggregation.

If this is the correct explanation then in habitat containing abundant good-quality burrowing soil less aggregation and a higher rate of burrow creation would be expected. This is exactly what was discovered by Cowan and Garson (1985) in their sand dune site, an ideal habitat for creating large and deep burrows in. The long-term use of warrens is another indication of habitat shortage (Hoogland, 1981), and many rabbit studies have noted a lack of new colonies being formed throughout study periods (Lockley, 1964; Mykytowycz & Gambale, 1965). Additionally, female philopatry has been suggested as being associated with a lack of nearby vacant territories (Künkele & von Holst, 1996). However, this theory is negated by the findings of the present study: large burrows in open areas but comparatively smaller ones in covered areas. This cannot be explained by the theory of habitat shortage as it is improbable that there would be a general pattern of habitat shortages in open areas but not in covered areas.

Possibility 4: Colonisation risk

The costs of colonisation could mean that a subordinate rabbit is often better off expanding an existing warren, even though long-term costs will have to be paid. It has previously been stated that both exposed and covered habitat pose the risk of predation to *O. cuniculus*. However there is abundant evidence revealing that a wide range of species dislike being far from cover (Hughes & Ward, 1993; Lima et al. 1985; Kotler, 1984) indicating that cover often conveys superior security. For rabbits, dispersal through certain matrices is undoubtedly perilous (Künkele & von Holst, 1996), and the exposure to predators whilst creating new burrows places a rabbit at greater risk from predation. This fact is highlighted by the common observation that rabbits are rarely seen to dig new warrens, much preferring to inhabit disused ones (Lockley, 1965).

Cowan (1987) came to the conclusion that group living in rabbits is the result of aggregated nest sites rather than social behaviour. The results from this study suggest that this aggregation is in turn the result of certain environments posing too many threats to promote colonisation away from existing warrens. Thus, in exposed sites the danger of venturing away from the protection of a burrow results in reduced and restricted natal dispersal, with individuals relinquishing the advantages that solitary living would otherwise have yielded them. In other words the perceived vulnerability from predators influences a rabbit's mode of living. This highlights the important role that predation can play in maintaining group living. Although rabbits can commonly be found living in 'social units' (Lee, 1994) they do not fit the definition of a social group: "animals that actively seek the proximity of each other...". Rather they co-occur "- in the same spot because of an attraction to the same environmental condition or factor..." (Krause & Ruxton, 2002).

4.3 Conclusion

The colonisation risk hypothesis, as presented above, offers the best explanation for the findings of the present study and previous ones conducted. Importantly, it justifies Cowan's findings that rabbits receive no benefits from group living whilst also explaining the findings presented in this paper: the distinction between warren

sizes in exposed and covered habitats. Thus the conclusion justifies how group living is maintained in the absence of no net benefits.

This investigation has implications for other studies that have presumptuously named species as being social. The European rabbit has often been labelled as a social creature, however this study has concluded that evidence indicates otherwise. An interesting study on redwinged blackbirds (*Agelaius phoeniceus*) in North America discovered no net benefits of group living, opposing previous reports (Weatherhead & Sommerer, 2001) and thus substantiating the possibility that group living is not necessarily an evolved lifestyle. Many studies fail to measure lifetime breeding success, which is essential if the results are to be meaningful. Any benefits found in studies using inferior variables will not necessarily outweigh the disadvantages and thus if costs still offset benefits then true sociality will not evolve.

Rather than being naturally sociable creatures, rabbit behaviour is comparable to that of the solitary hare. Both increase their levels of vigilance with increasing group size, indicating that the net benefits obtained from solitary living must be actively preventing the natural selection of behaviours commonly associated with gregarious species, and both have strong hierarchies within any group that may form (Monaghan & Metcalfe, 1985). Increasing our understanding of the European rabbit is important if future control methods are to prove successful. *O. cuniculus* poses a lethal threat to the fragile biodiversity of countries such as Australia and New Zealand. Unfortunately attempts at eradication have so far been ineffective. Despite the lack of data collected in this study (with eight sites being studied per habitat type) and the conservative sampling method used significant differences were still found between open and covered sites. This indicates that further research into the subject area would bring important corroboration to the theory presented here, thus providing a strong foundation for any future studies.

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