

3. The Behaviour and Ecology of *Rattus norvegicus*: from Opportunism to Kamikaze Tendencies

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Abstract

While rat population management is clearly possible in the absence of a knowledge of rat biology, we aim to show in this review how control is likely to prove more effective if woven into a robust framework of understanding. For example, rats have flexible population dynamics and can delay the onset of fertility in times of food shortage. Detailed observations have demonstrated the presence of stable, near-linear dominance hierarchies, where male social status tends to be age-related. We discuss how the success of poisoning strategies are crucially dependent on the foraging decisions which are made against this background of dominance hierarchies and competition for mates. Feeding patterns also can be altered in order to avoid predators. Rats are notoriously neophobic, and poor bait uptake is one of the main reasons that control strategies fail. Our review highlights the importance of social cues and *Toxoplasma gondii* infection in the modulation of neophobic responses. The potential impact of ill-planned rat control operations on the spread of zoonotic diseases is also considered. Finally, we discuss the development of behavioural and physiological resistance by rats in the face of continued poisoning pressure, and the apparent evolution of a new type of resistance which benefits the rat even in the absence of poison.

Keywords

Rattus norvegicus, rats, behaviour, society, neophobia, resistance, disease

INTRODUCTION

EXplosive demography, adaptable ecology and opportunistic behaviour are capacities that cause rats to rank high amongst those mammals that have most affected the course of human history. Today rats exact an immense toll on society worldwide, whether through the costs of prophylactic or remedial control, or through disease transmission and damage to crops and stored food. Throughout Southeast Asia, for example, pre-harvest damage caused by the rice-field rat, *Rattus argentiventer*, is reckoned to reduce crop yields by 17%, a figure which translates into the squandered rice requirements of in the order of 20 million people (Singleton 1997). Such losses may also have indirect environmental costs; lower yields forcing larger areas into production and accelerating the cultivation of wilderness with consequent threats to biodiversity. More directly, rats threaten the survival of endemic fauna on a number of islands, from the Galapagos to Guam (e.g. Amarasekare 1993; Robertson et al. 1994; Cree et al. 1995); alien species are, second only to habitat loss, the greatest contemporary force for extinction. Finally, the enormity of the threat posed to humanity by rat-borne disease is heightened in the context of our huge populations, rapid transportation and antibiotic resistance. Amongst the emerging infectious diseases, the viral haemorrhagic fevers and Lassa fevers add to the already lengthy list of blights which can be transmitted by rodents. The 200,000 cases of haemorrhagic fever with renal syndrome

diagnosed annually in Asia is doubtless just the tip of an epizootiological iceberg. These threats are not confined to the developing world: the 1973 wave of deaths through hantavirus with pulmonary syndrome amongst healthy young Americans led to the discovery of hantavirus in the deer mouse, *Peromyscus maniculatus* (Childs et al. 1987). Hantavirus infection has also been discovered in Norway rats in rural Britain (Webster and Macdonald 1995a).

Amongst the diversity of problems caused by rodents, the Norway rat (*Rattus norvegicus*), ranks high amongst the miscreant species. Originally from Southeast Asia, the Norway rat's versatility rivals mankind's and our two species have, in company, spread around the globe. Trawling bibliographic indices reveals that some 24,000 technical publications refer annually to *R. norvegicus* (Berdoy and Macdonald 1991). This stunning total is, however, neither a fitting tribute to the fascination of its adaptability nor recognition of the enormity of its pest status; rather it stems largely from the utility of its domestic form as a model for studies ranging from biochemistry to experimental psychology. Publications on wild-type Norway rats largely concern toxicological studies of candidate poisons, while the behaviour and ecology of the species in the wild—which is where it actually does damage—account for scarcely a handful of those 24,000 publications annually. Indeed, as we shall show, while a little is known of the ecology of wild rats in farmscapes and a few cities in a smattering of developed countries, they are perversely unstudied where they impact the most. Most startling

of all, effectively nothing is known of the biology of the sewer-dwelling rat.

Our objective in this chapter is to review the behavioural ecology of wild rats, largely within the context of our own team's findings. Our contention is that while rat control is manifestly possible in the absence of much knowledge of rat biology, it is likely to be much more effective if woven into a robust framework of understanding. This proposition rests on the oft-proven wisdom of the maxim: 'know thyn enemy'. In particular, our aim is to reveal that seemingly disjunct, and perhaps even rarefied, research topics, such as dispersal, social status, feeding patterns and disease transmission are actually inextricably linked in formulating a biological basis for rat management.

POPULATIONS, DEMOGRAPHY AND DISPERSAL

Questions about the population biology of Norway rats were at the forefront of mammalian ecology in post-war years, thanks to the pioneering work by Elton and Chitty (Chitty 1954) and Davies (1949). Considering the enormity of the rat's agronomic and public health impact, it is remarkable that the momentum of these early investigations was soon dissipated.

Numerous studies on farmland (Errington 1935; Aisenstadt 1945; Emlen et al. 1948; Zapletal 1964; Hartley and Bishop 1979; Brodie 1981; Huson and Rennison 1981; Homolka 1983) in differing temperate climates indicate that hedges and fields are generally a marginal habitat for rats, except when crops are available as food. Middleton (1954) noted that all rat infestations in

hedgerows at his study site in Berkshire (United Kingdom) were either short-lived or were associated with rat colonies in corn-ricks or field-barns. He suggested that scattered field colonies were themselves ephemeral, but were probably the main reservoirs from which infestation of farm buildings occurred in the autumn and winter.

Colonists tend to be rats that are approaching, or have recently achieved, sexual maturity (Zapletal 1964). Telle (1966) found that most colonists weighed between 160–250 g, while Farhang-Azad and Southwick (1979) reported a mean weight of 190 g for 26 rats collected from newly recolonised burrows. Both concluded that emigrants are mainly young animals, but neither reported the sex of new colonists. However, Bishop and Hartley (1976) found approximately twice as many 'new' adult males as females entering their hedgerow population. Similarly, Calhoun (1962) reported that more males than females were ejected, or at least departed, from more socially stable colonies. Kendall (1984) and Leslie et al. (1952) found that the sex ratio of rats in environments where they breed tended to be biased towards females.

Rat population dynamics, and thus the success of control operations, are intimately linked with the availability of food supplies. In the simplest case, bait uptake is most likely when other sources of food are unavailable. However, we have found that food supply, and other environmental factors, also produce concomitant changes in behavioural and reproductive ecology (D.W. Macdonald and M.G.P. Fenn, unpublished data). These changes in turn may be of fundamental importance to rat population

size and to control efforts. We live-trapped and radio-tracked rats in three contrasting United Kingdom farmland habitats, all of which were surrounded by winter wheat: (i) a resource-rich agricultural tip; (ii) a woodland where grain was intermittently provided for pheasants; and (iii) an adjacent, resource-poor stream bank. Several salient findings emerge. First, and unsurprisingly, more rats occurred at the farm rubbish tip, where food was most abundant, and fewest along a stream where it was most scarce (Figure 1). Second, numbers varied at each site: in general, there was a cycle in rat abundance corresponding to seasonal

changes in breeding activity—pregnant females were generally captured from March until October, and peak numbers of juveniles were found between November and December (see also Davies and Hall 1951; Farhang-Azad and Southwick 1979, who report a bimodal pregnancy rate, with highs in spring and late summer). There is also evidence that reproduction ceases in cold winters (Leslie et al. 1952; Andrews et al. 1972; Lattanzio and Chapman 1980). However, in our study (D.W. Macdonald and M.G.P. Fenn, unpublished data) breeding activity was not simply a function of season but also depended on food

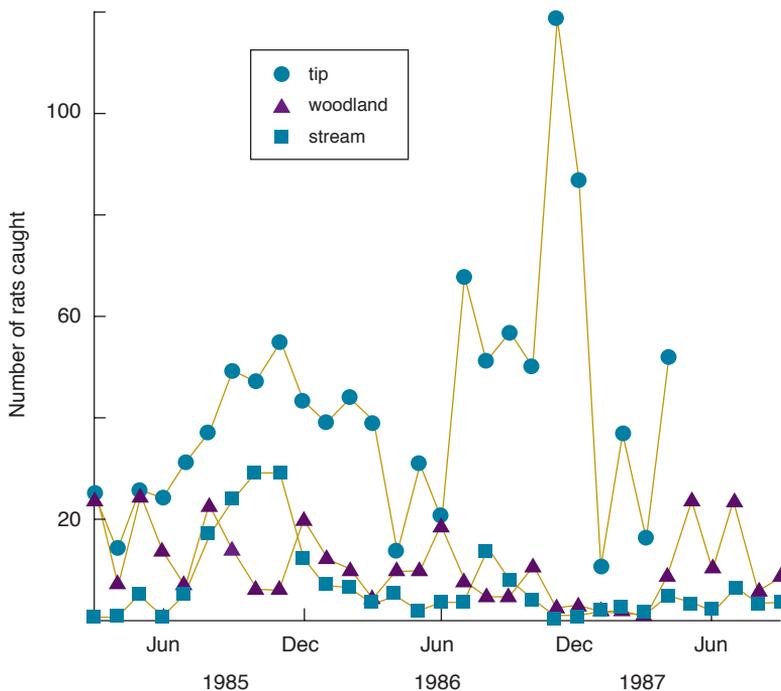


Figure 1.

Variation in rat abundance across time in three habitats with different food resources. The figure illustrates that more rats were captured in the resource-rich environment of the tip than in the woodland (moderate food availability) or stream (poor availability of resources). Cyclical fluctuations in abundance were also more marked in the resource-rich environment (D.W. Macdonald and M.G.P. Fenn, unpublished data).

availability. In the woodland site, winter breeding was stimulated by the provision of grain in January for the pheasants, with peak numbers of juvenile rats occurring in the population approximately three months later, in March and April.

Fertility in both sexes was affected by season. Using perforation as a measure of attainment of sexual maturity, the median weight of females at perforation at the rubbish-tip site was higher in the summer sample than the winter one. Fertility in males was also modulated by season and food supply, with evidence for delayed onset of sexual maturity and facultative cessation of spermatogenesis where food was scarce. For example, males achieved a greater weight before their testes became scrotal in winter than was the case in summer. Similarly, those animals living in the relatively poor environment of the stream delayed sexual maturity until they had achieved a greater weight than their counterparts in more productive habitats (Figure 2) (D.W. Macdonald and M.G.P. Fenn, unpublished data). Indeed, it was not unusual for males weighing more than 300 g to have abdominal testes [the median weight of rats with scrotal testes reported elsewhere was 136 g in rural rats (Davies 1949) and 145 g in rats living around Baltimore zoo (Farhang-Azad and Southwick 1979)]. Clearly, the control of food availability may have an important role in maintaining rat populations at manageable levels.

Movements

Farmland rats may either occupy stable home ranges or travel widely as transients. Hartley and Bishop (1979) estimated that three-quarters of rats fell in the former

category and therefore were unlikely to have access to bait points positioned outside their home ranges. Within the home range, rats regularly retreat to rest sites (Orians and Pearson 1979; Galef 1988), which in arable areas tend to be located in hedge bottoms and banks (Brodie 1981).

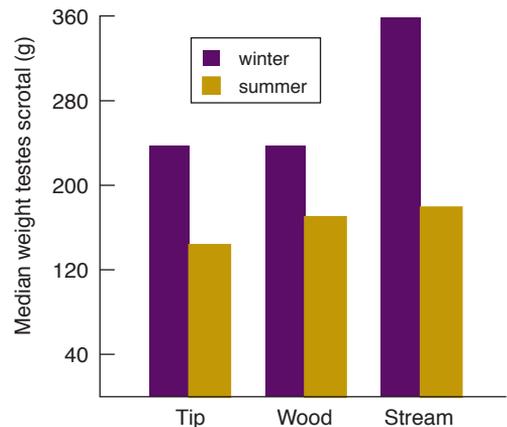


Figure 2. Median weight at which testes became scrotal in winter and in summer at sites which differed in resource availability (tip = resource rich, wood = moderate, stream = poor). The figure illustrates that males achieved sexual maturity at lower weights in summer than in winter, and also in resource-rich environments ($p < 0.05$ for seasonal differences, $p < 0.001$ for resource differences) (D. W. Macdonald and M.G.P Fenn, unpublished data).

We radio-tracked rats in and around farms (Fenn et al. 1987; Macdonald and Fenn 1995). Males ranged widely through the fields when crop cover was available to provide protection from predators [mean linear home range = 678 m, standard deviation (SD) = 535]. However, their ranges contracted after harvest (90 m, SD = 28.2). This effect appeared not to apply to females,

which generally had smaller home ranges. In addition to farming activity, the absolute availability of food also influenced home range size.

Females at the Wytham tip, where food was plentiful, had linear ranges averaging only 85 m whereas those based in the relatively poor environment of the stream had a mean home range of 428 m. Similar results were observed for males (see also Taylor 1978; Hardy and Taylor 1979). Clearly, home range is likely to vary greatly with circumstances.

Social system

The seminal study of rat society was undertaken by Calhoun (1962) working with rats in an outdoor enclosure. He concluded that social pressures were important in the movement of rats and, specifically, that subordinate males were forced to migrate into less favourable sites, leading to an unbalanced sex ratio (as low as 0.38) in good habitats. Similar reports of unbalanced sex ratios in areas suitable for breeding have also been made by others (e.g. Leslie et al. 1952). This socially-induced migration away from good sites may explain the transient infestation of fields and corn-ricks often reported during the summer. Social dominance confers feeding priority (Smith et al. 1991a), greater reproductive access and success (Gärtner et al. 1981; McClintok et al. 1982; Adams and Boice 1983, 1989) and reduces susceptibility to adverse conditions (Barnett 1955, 1958a; Christian and Davies 1964; Boice 1969).

We radio-tracked rats at our three farmland study sites (D.W. Macdonald and M.G.P. Fenn, unpublished data), and various other farm situations (Fenn et al.

1987; Fenn and Macdonald 1987). In summary, where resources were abundant and clumped, rats formed multi-male, multi-female groups which we suspect defended a clan territory. In areas with scattered or sparse resources, male movements were consistent with exclusive male ranges with access to several females. Insofar as any spatial exclusivity would affect access to baiting stations, the spatial organisation of rat populations is clearly important to poisoning operations. On one farm we found that almost all radio-tracked rats visited a particular grain mill at some stage; when poison was placed there an estimated 95% of the population was killed (Fenn et al. 1987).

The sex ratio of the populations along the stream was constant, and equal, throughout the year. In contrast, in the wood (around the pheasant hoppers) the sex ratio was significantly skewed: only approximately one fifth of rats captured between January and June were male [$\chi^2 = 5.828$, degrees of freedom (d.f.) = 1, $p = 0.016$ from January–March; $\chi^2 = 11.765$, d.f. = 1, $p = 0.0006$ from April–June]. We conclude that where groups developed around reliable food supplies, resident males excluded transient incomers, whereas these were numerous in passage through the poorly resourced stream habitat.

In order to examine further the consequences of ecological variation on social structure, we observed several colonies of wild Norway rats housed in large outdoor enclosures (c. 266 m²). In an effort to bring the field into the laboratory, we provided rats with problems which they would encounter in the wild, including sufficient space, a diverse and multi-generational social environment and a dispersed food supply. Nocturnal

observations showed that rat colonies were organised into steady, near-linear dominance hierarchies where male social status tended to be age-related (Berdoy et al. 1995a). Larger rats stood a better chance of winning contests, particularly when interacting with unfamiliar individuals, (Figure 3a). But social status within colonies became fixed: the results of earlier encounters appeared to determine the outcome of future ones, and dominant individuals thus maintained their social status long after initial body weight asymmetries with younger individuals had disappeared or even been reversed (Figure 3b). In stable groups, therefore, age is often a better predictor of social status than is size, with the alpha male being smaller than many of its subordinates (see also Calhoun 1962). Such 'settled dominance' (Berdoy et al. 1995a) may be found in a variety of other species (e.g. American bison, Rutberg 1983, but see Wolff 1988; red deer, Thouless and Guinness 1986; blue-footed booby chicks, Drummond and Osorno 1992; see also Huntingford and Turner 1987, for discussion of endocrine consequences of fighting). In rats it may explain why, despite considerable attention, the evidence that dominance is correlated to body weight has been conflicting—e.g. Barnett (1958a), Boreman and Price (1972), Nott (1988) and Smith et al. (1994) found a positive relationship whilst Baenninger (1966, 1970), Boice (1972), Price et al. (1976) and Sridhara et al. (1980) did not.

Why do large subordinates seem to accept the status quo rather than challenging smaller dominant individuals? We suspect that the costs of escalated aggression are great relative to the value of the contested

resource. Whilst adult male rats were obviously in competition for food and mates, even the lowest subordinates could achieve access to feeding sites by adapting their feeding patterns accordingly (Berdoy and Macdonald 1991; Berdoy 1994). Moreover, dominant males could not monopolise access to oestrous females (Berdoy et al. 1995b).

In one colony, observations showed that whilst the alpha male enjoyed the highest number of copulations, there was no straightforward correlation between social status and mating success, with some subordinates achieving more copulations than individuals far higher in the dominance hierarchy. In another colony, the dominant male actually had less mating success than his two immediate subordinates.

This state of affairs is likely to be a consequence of the rat's mating system and may even be encouraged by the female's behaviour. Observations in the naturalistic environment of our enclosure colonies showed that mating was achieved by a type of scramble competition. Males pursued the oestrous female wherever she moved outside her burrow. Females were typically in oestrus for one night only, during which they were assiduously followed by a string of two to three males (up to seven), and mated repeatedly with several of them. Importantly, males had little time to interact with each other during the pursuit of oestrous females because they would lose a mating opportunity, and as a consequence even the most dominant males could not monopolise access to the female.

The scramble amongst males to mate with a female was so intense that it was hard to detect whether females displayed any

Figure 3. (a)
The effect of body weight asymmetry on social dominance in 132 pairs of adult male rats. There was a significantly increasing effect of weight on the chance of winning contests as the weight/age asymmetries between contestants became larger ($G = 20.17$; d.f. = 4; $p = 0.0003$). Asterisks show the statistical significance of weight asymmetry on the likelihood of winning a contest within each weight asymmetry class (ns = non significant, * = $p < 0.05$, ** = $p < 0.01$, * = $p < 0.001$, using binomial one-tailed test).**

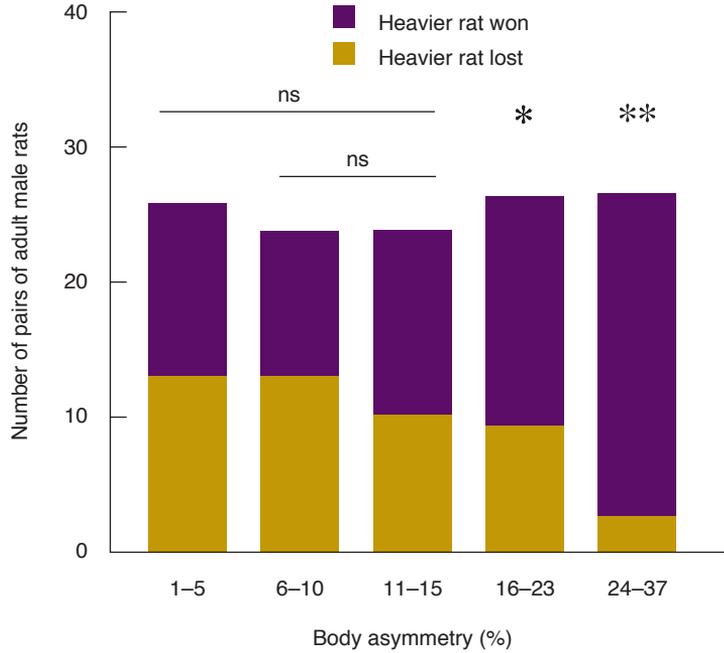
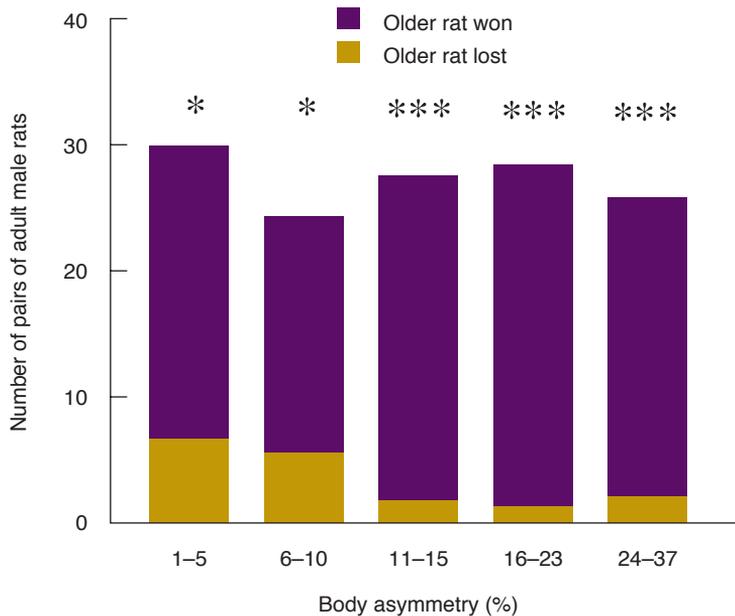


Figure 3.(b)
The effect of age asymmetry on social dominance in 132 pairs of adult male rats. There was a significantly increasing effect of age on the chance of winning contests as the weight/age asymmetries between contestants became larger ($G = 12.48$; d.f. = 4; $p = 0.014$). Asterisks show the statistical significance of weight asymmetry on the likelihood of winning a contest within each weight asymmetry class (ns = non significant, * = $p < 0.05$, ** = $p < 0.01$, * = $p < 0.001$, using binomial two-tailed test).**



mate selection or whether they mated promiscuously from choice.

To test these possibilities we devised an apparatus which exploited the sexual dimorphism in size amongst rats; male rats were housed in cubicles around a central arena in which a female was placed. A circular passage permitted the female access to each male's cubicle, but was too narrow for the male to pass (M. Berdoy et al., unpublished data; C. Rolland et al., unpublished data). Observations in this 'inverta-brothel' enabled us to see that females clearly exercised mate choice. Liberated from the constraints of male–male competitive behaviour, females formed enduring bonds with a single male, but nevertheless selected to mate promiscuously (although to a lesser extent) with a small number of the males available to them.

Social odours

There is a huge literature on olfactory communication amongst rats (e.g. see reviews in Brown and Macdonald 1985). Following observations of the males' assiduous sniffing of females in our enclosures, and their pursuit of those in oestrus, we began to question the significance of haunch odour. The scent of rat haunches had at least 22 volatile components, the proportions of which varied greatly between individuals. Although no single compound emerged as diagnostic, principal component analysis revealed exclusive categories in the odour profiles of males, oestrous females and dioestrous females, with the first axis explaining 80% of the variation. Haunch odours could, therefore, be separated along biologically meaningful lines, suggesting that they had the potential to signal useful

information to rats (Natynczuk and Macdonald 1994a,b).

In order to receive an olfactory signal, rats must smell the encoding odour. We have investigated 'sniffing behaviour' in a group of 62 adult rats (Natynczuk and Macdonald 1994a,b). Male rats sniffed frequently at the various body zones of females but there were significant differences in the proportions of sniffs directed to the various body zones ($F = 38.21, 32, 28$ d.f., $p = 0.005$). The highest proportion of sniffs (23%) were to the females' haunches, and this behaviour was seen whether or not the female rat was related or in oestrus. However, the genital region of non-related oestrous females was investigated significantly more frequently (29% of all sniffs) than the genital region of any other group ($\chi^2 = 4.642, 1$ d.f., $p = 0.031$ for difference in proportions of sniffs for non-related oestrous and non-oestrous females). Males tended to sniff the haunch after sniffing the forequarters, as part of a sequence of sniffing along the female's body from forequarters to hindquarters. Histology of the skin sebaceous glands indicated that the secretory activity of glands in the haunch, but not those in the forequarters, changed during oestrus (Natynczuk and Macdonald 1994a,b; Natynczuk et al. 1995). A male rat will therefore smell a discontinuity or gradient in scent along the body of an oestrous female but not a dioestrous female. Rats can thus judge a female's reproductive status by calibrating the odour of her haunch against that of her forequarters.

The self-calibration model has four advantages: (a) it obviates the need for learning or inheriting responses to a

pharmacopoeia of scents; (b) it minimises the difficulty posed to the recipient by variation, in quality and quantity, between the odours of different signallers; (c) social odours are inevitably mixed with variable and copious background smells, and even one individual's scent may vary over only a few days; and (d) it could work not only with complex mixes of chemicals, but also with single compounds. Self-calibration relies on assessment of the degree of difference between odours for the transmission of a signal and therefore might apply to a variety of phenomena detailed in the literature (Natynczuk et al. 1995). It is currently unclear whether a strategy employing pheromones could be used to disrupt rats mating systems and hence control population size.

FEEDING BEHAVIOUR

Foraging decisions must be carried out against a background of dominance hierarchies and competition for mates. A foraging rat must make decisions about when to feed, how to structure foraging bouts within its period of activity, and what to eat. Clearly an understanding of foraging behaviour is crucial to the development of more effective baiting systems: neophobia, food preferences and conditioned aversions associated with illness may all limit bait uptakes. As Quy et al. (1992a,b) and Cowan et al. (1994) point out, rat control operations often fail because of poor bait uptake.

Feeding decisions

Most wild rat populations are essentially nocturnal (Calhoun 1962; Taylor et al. 1991; Berdoy 1994) and therefore face two related

problems. First, there is significant seasonal variation in the period for which they must fast during daylight hours. Second, and correspondingly, they must satisfy their energy requirements during nights of variable duration. The shorter the night, the more likely there is to be a conflict of interest between feeding and mating, which is also at its peak during the shortest summer nights. We attempted to determine how these conflicts are resolved.

Long-term monitoring of feeding activity in our colony of wild rats, using a purpose-built, continuously recording telemetric device (Berdoy and Evans 1990) showed that the adjustment in feeding intensity to maintain nocturnality (which rose by 65% between December and June as nights grew shorter) was not uniform (Berdoy 1994). Rats mainly compensated for the seasonal reduction in feeding time by increasing feeding activity during the last quarter of the night (Figure 4). As a result, the distribution of feeding activity through the night gradually changed from being roughly constant in winter (and comparable to that obtained in the laboratory) to being clearly skewed in summer, with a sharp peak of activity before sunrise. Feeding during the earlier part of the night remained at the same intensity as in winter. Since food availability was kept constant throughout the year why did the timing of feeding activity change so drastically between winter and summer?

First, during the first half of the night, the rats were generally busy exploring the enclosure and engaging in social activities. In males, the disruption of feeding was related to the intensity of mating effort which could result in little or no feeding at the beginning of the night. Such disturbance

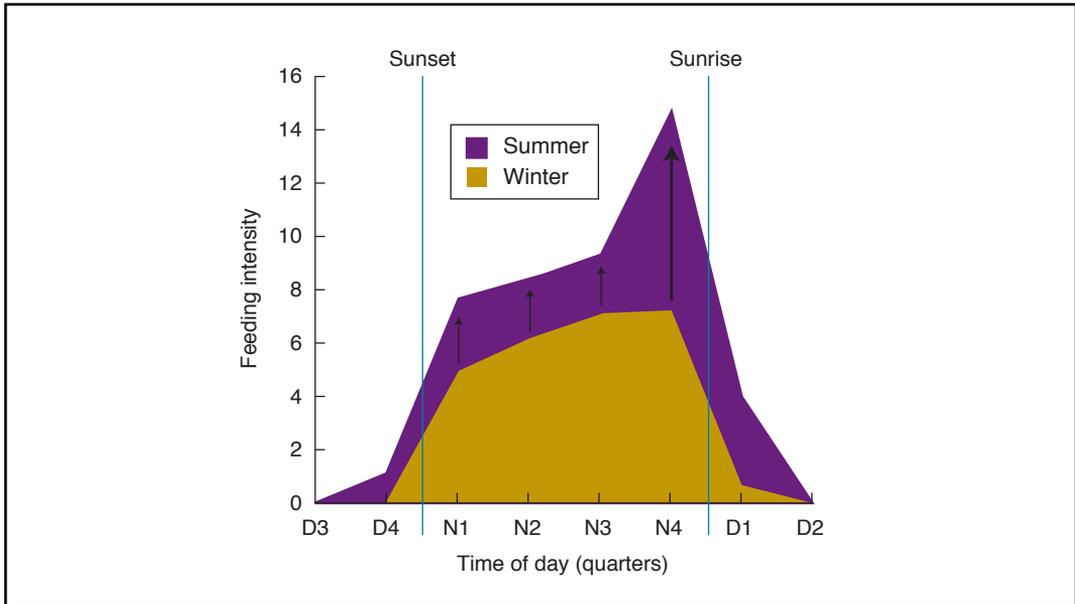


Figure 4.

Non-uniform increase in feeding activity in response to shorter summer nights. To control for the 50% reduction in night length between summer and winter, the data for day and night periods have been divided into quarters (Day = D1–D4; Night = N1–N4). The significantly greater increase in feeding intensity during the last quarter of the night (N4, thick arrow) causes an increasingly skewed feeding distribution during short summer nights. Note also the greater proportion of dawn feeding (D1) during summer.

was greatest during the summer when oestrous females were most numerous. Whereas the feeding activity of an oestrous female was principally disrupted for that night only, the presence of an oestrous female affected the feeding activity of each courting male in the colony.

Second, rats may have foraged mainly during the last portion of the night to time their feeding activity in anticipation of subsequent energy needs (Le Magnen 1985). Presumably rats needed to gather reserves that allowed them to last until the following night, particularly during periods of long daylight hours. Analyses showed that 90% of the monthly changes in the timing of activity in females, which were less

disrupted by social living than were males, could be explained in terms of seasonal variation in night length.

Predator-altered behaviour

Whilst radio-tracking wild rats on farms around Oxfordshire, we identified an intriguing population of diurnal rats (Fenn and Macdonald 1995). The rats occupied a midden on one of five study farms. Coincidentally, a particularly large number of signs of the red fox (*Vulpes vulpes*) were also discovered in the vicinity of the midden, but were more or less absent from the other four sites, at which rats were typically nocturnal. We had previously found that

wild-caught rats kept in enclosures modified their foraging behaviour in order to avoid areas scented with fox urine, whereas their activities were unaffected by rabbit urine (Berdoy and Macdonald 1991; see Vernet-Maury et al. 1968, 1984 for studies on odorants inducing stress in laboratory rats—some found in fox faeces). We therefore hypothesised that the rats at the midden were diurnally active in order to avoid fox predation. Establishing a direct effect of predation, however, required careful study to eliminate two other equally plausible explanations. First, the activity observed could have been that of low-ranking animals, forced to be diurnal to escape competition with dominants (a phenomenon observed in our enclosures—Berdoy 1994). Second, diurnal behaviour might have been facilitated by the lack of human disturbance at the site (see Taylor 1975).

Infra-red photo-electric cells revealed that the rats were active only when the foxes were absent. Seasonal use of the midden by foxes meant that the risk of predation to rats was greatest in summer, and correspondingly, the rats were most strictly diurnal in summer. The next step was to go beyond the correlational nature of the existing data. A fox-free enclosure was built near the midden and stocked with rats from the diurnal population. Rats in the enclosure should have been able to detect the absence of foxes though the lack of odour from fox urine and faeces. If rats were diurnally active to avoid fox predation, then in the absence of foxes we expected them to revert to nocturnal behaviour. This was exactly what happened (Fenn and Macdonald 1995). In contrast, disturbance alone, such as human

and traffic activity at night, does not appear to interrupt the foraging activities of urban rats (Takahashi and Lore 1980).

Interestingly, foxes visited the midden primarily to scavenge on farm waste rather than to feed on rats. Thus the presence of one prey type (scavenge) increased the mortality risk to another prey type (rats).

Meal patterns

Rats feed in bouts, so the adjustment of food intake to calorific expenditure must be achieved through variation in the size and the frequency of meals. For example, females forage in many short visits, whereas males use fewer, longer ones (Inglis et al. 1996). We therefore examined how the structure of feeding itself is influenced by variable night length and social pressures (Berdoy 1991, 1994). The feeding patterns of rats in the laboratory tend to show a positive relationship between the size of a meal and the following inter-meal interval (referred to as a 'post-prandial correlation'), but not between the size of the meal and the interval separating it from the previous one (a 'pre-prandial correlation') (Figure 5) (see Le Magnen 1985 for a review).

Colloquially, this means that rats decide on the size of a meal on the basis of how hungry they expect to be, rather than how hungry they are (Snowdon and Wampler 1974; Le Magnen 1985). A post-prandial correlation in an individual's feeding pattern is generally thought to indicate that the individual has good control of the onset and termination of its meals. On the other hand, an animal that is less able to control the onset of feeding than its termination is more likely to exhibit pre-prandial correlations. These principles have been useful in elucidating the

physiology of feeding in the laboratory, but they also provided a tool for our investigation of the complex feeding patterns of rats under natural circumstances. Following Slater (1981), we tested the hypothesis that in predictable environments (such as in our enclosure) individuals would be more likely to exhibit post-prandial than pre-prandial correlations. Subordinates, on the other hand, which may be less likely to control the onset of feeding due to disturbances by dominant individuals, would effectively be living in an uncertain environment and should be more likely to exhibit pre-prandial correlations than would dominants. If so, subordinate and dominant rats might respond differently to baiting programs.

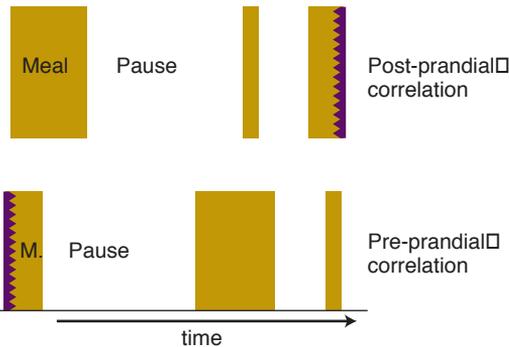


Figure 5. Types of feeding pattern which reflect a food intake regulated from meal to meal. The upper part of the figure illustrates a positive correlation between the size of meal and the following pause. The lower part of the figure shows a positive correlation between size of meal and the preceding pause.

We analysed the feeding patterns of 12 adult rats (Berdoy 1991, 1993, 1994; Brunton 1995). First, the intervals between meals in the colony of rats appeared, on the whole, to be dependant on the size of the preceding meal

(post-prandial correlation). Thus, knowledge of the length of time for which a rat had not eaten was, counter-intuitively, a poor predictor of the size of the next meal. Meal size appeared instead to be a reflection of the rat's anticipated subsequent energy need. Second, the consequences of agonistic and mating behaviour were also reflected in the values of these relationships. As predicted, dominant males, who benefited from a greater freedom of access to the feeding sites, and females (who were less disrupted by agonistic behaviour and matings than males), tended to regulate their feeding more closely than their subordinates or male counterparts (see also Slater 1981). Moreover, post-prandial correlations were more apparent in winter than in summer, supporting the idea that they were less able to regulate their meals when mating was at its peak and activity was skewed towards a pre-dawn peak.

The extent to which dietary decisions depend upon the fine structure of feeding, and the consequences of individual variation—let alone seasonal variation—on diet selection are rarely considered in the literature on rat nutrition. Yet these differences not only constitute the basis on which natural selection operates, but they may also relate to the way in which dietary decisions are made (Tempel et al. 1985; Hayne et al. 1986). They therefore affect the capacity for diet selection in general, and for aversion learning in particular.

Neophobia

Thompson's (1948) early work clearly demonstrated neophobia in wild rats in response to both new food and to lighting used to observe his experimental site (see also Barnett 1958a; Cowan 1977; Miller and

Holzmann 1981; Beck et al. 1988 and review in Royet 1983). To overcome neophobia, pre-baiting is now an integral part of most rat-poisoning operations. The function of neophobia remains unproven, and it may have more to do with a general timidity than with food selection. However, while neophobia is likely to incur the cost of avoiding potentially harmless foods, it may facilitate the rat's ability to associate eating a novel food with adverse effects sometime later (Rozin and Kalat 1972; Nachman and Hartley 1975; Rescorla 1980: ability to associate illness with toxic food). Given the wide range of food qualities which a rat may encounter, and the intensity of poisoning pressure to which it is subjected, neophobia is generally assumed to be of adaptive significance (Rozin 1976). Indeed, neophobia was found to be absent amongst rats of the Hawea and Breaksea Islands, New Zealand (Taylor and Thomas 1993) which were historically uninhabited. In general, non-commensal rodent species also only show weak neophobia (Cowan 1977; Brammer et al. 1988). The transition from feeding from familiar to novel food after a period of neophobia is usually a gradual process (Chitty 1954; Barnett 1975). Wild rats may initially only sample a small amount of the food with amounts taken gradually increasing (Thompson 1948; Shepard and Inglis 1987; but see Beck et al. 1988).

It is difficult to quantify neophobia in rats in the field, because of the large number of potential confounding variables. We therefore designed a series of experiments to measure neophobic responses in wild-caught rats. The first of these housed rats in large outdoor colonies (Berdoy 1994). The rats avoided familiar foods (on which they had

been fed ad libitum for two years) in a familiar feeding box when the grain was scented with natural oils. This reaction was still significant after 40 days. Even more extreme neophobia was noted when a novel food was presented. Inglis et al. (1996) undertook a similar study, but his rats were housed in concrete arenas and did not have lower intakes of novel foods, or of unfamiliar foods (foods which had previously been familiar, but had not been offered to the rats since they were caught). However, the rats did make more visits to the new foods, consuming less per trip. In contrast, the introduction of a novel food bowl, even though it contained familiar food, elicited strong neophobic responses, reducing food intake to 5% of its previous level. This neophobia, while diminished, was still evident after five days (Cowan 1976 reports similar results for the black rat, *Rattus rattus*, see also Galef and Heiber 1976; Galef 1988).

We investigated whether rats of different provenance displayed different levels of neophobia. In particular, we compared the behaviour of rats which had recently survived intensive poisoning on a Welsh farm with those which had been in the protected milieu of our enclosure for two years (Brunton and Macdonald 1996). The enclosure rats were descended from the survivors of a poisoning treatment in Hampshire two years previously. Hampshire rats had proven notoriously difficult to poison (Richards 1981; Greaves et al. 1982a,b; Quy et al. 1992b), prompting the hypothesis that they might be unusually neophobic. We designed three trials to test this. First we tested the effect of an unfamiliar odour on a familiar object (this involved handling the food container

without gloves). Next, we tested the effect of replacing a familiar food container with a novel container while food and odour remained constant. Finally, we tested the effect of placing a novel food in a familiar container. In each case a familiar bowl, containing familiar food, was present throughout. The latency to feed, when confronted with each form of novelty, was allocated an ordinal score to indicate the degree of neophobia. The summed results from the three experiments were then used as to create a 'neophobia index'. A score of 0 indicated no neophobia and 6 indicated extreme neophobia.

The survivors from the readily controlled Welsh populations were significantly more neophobic than enclosure rats descended from the problematic Hampshire population. Nonetheless, within both the Hampshire and the Welsh groups were some individuals that showed no neophobia (8% and 10%, respectively), and others that showed extreme neophobia (an index of 6: 4% and 10%, respectively) (Figure 6).

Perhaps the Welsh farm rats were a sample of the most neophobic individuals from the original population, the less neophobic rats having been selected out by poisoning. The rats born in the enclosure, although descended from the survivors of a poison treatment, had not themselves been subject to selection by poisoning and we hypothesise that they contained the full range of neophobic phenotypes. Thus, the differences in neophobia between the two groups is likely to be due to the presence of a higher proportion of strongly neophobic rats in the wild-caught population (Richter 1953; Barnett 1958b; Mitchell 1976; Cowan 1977). The failure of poison treatments in

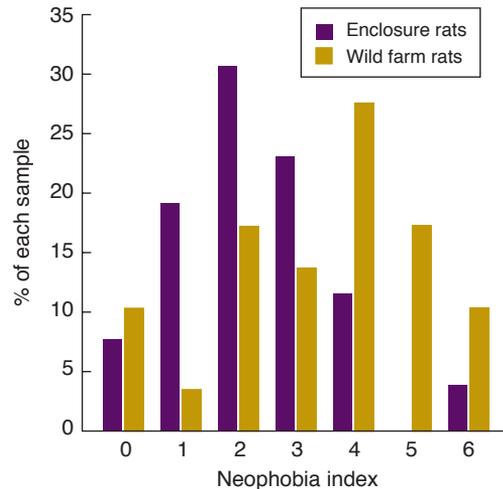


Figure 6. Percentage of wild farm rats (from populations considered normal to control; n = 30) and enclosure rats (descended from Hampshire rats; n = 30) at each index of neophobia, where a score of 0 indicated no neophobia and 6 extreme neophobia. Overall, the farm rats were significantly more neophobic (Mann Whitney U test $Z = -3.0$; $p = 0.009$).

Hampshire is therefore not explicable by a fundamental difference in the inherited level of neophobia. In fact, like Quy et al. (1992a), we concluded that the difficulty in controlling the Hampshire rats was most likely due to the stable and abundant source of food. Various studies suggest that the strongest neophobic reaction in wild rats is to new objects in a familiar environment (Shorten 1954; Cowan and Barnett 1975; Cowan 1976, 1977; Wallace and Barnett 1990); evidence is accumulating that neophobia is related to the stability of the environment (e.g. little neophobia in landfill site rats—Boice and Boice 1968) although unfamiliar areas with new objects are readily explored (Barnett and Spencer 1951; Cowan and Barnett 1975; Cowan 1977).

The interplay of conditioned aversion and innate neophobia is extremely complex. Indeed, neophobia may actually assist in the development of conditioned aversion, by making it more likely that a rat will remember eating a novel food, and thereby associate it with any adverse consequences. In the experiments with rats from Wales and Hampshire, the temporal patterns of feeding during the night were related to the rat's degree of neophobia (Berdoy 1994; Brunton 1995). Individuals that displayed no neophobia were more inclined than most to restrict their feeding to the end of the night. These associations are still largely mysterious. We can conclude, however, that subordinates may be constrained to eating shortly before dawn (Berdoy and Macdonald 1991) and may be more likely to try new foods than dominant individuals (Nott 1988). There is also evidence that the strength of taste aversions may be modulated by circadian rhythms (e.g. Infurna et al. 1979).

Social factors in food avoidance

Field studies have shown that rat colonies living in the same area can show substantial differences in food preferences not explicable by availability (Gandolfi and Parisi 1973). Subsequent laboratory studies have demonstrated that information about both the toxicity (the 'poisoned partner effect'—Bond 1984) and palatability of food can be transferred from mother to offspring, including via the mother's milk (Galef and Clark 1972; Hepper 1990). Diet preference can also be socially induced in adult laboratory rats (Galef and Wigmore 1983; Posadas-Andrews and Roper 1983). Thus, rats faced with novel foods are influenced by

the olfactory information emanating from another rat which has eaten at the novel food types (the 'demonstrator effect'—Ludvigson et al. 1985; Galef 1988, 1994). However, the response of the rats receiving these cues differs according to the state of the 'demonstrator', with a dead animal producing no effects on food selection. The position of the cues is also important: residues on the anterior of the rat, but not the posterior, will elicit a response in the 'observer'. These results make functional sense since the contextual clues which induce preference are those which corroborate the circumstantial evidence of what the 'demonstrators' have eaten.

We investigated the demonstrator effect in naturalistic circumstances by manipulating the olfactory information emanating from some individuals in one of two enclosure colonies and evaluating the consequences on the diet selection of other wild colony members (Berdoy 1994). In order to produce individuals that exhibited the characteristics of having eaten cinnamon-scented food, about a dozen drops of cinnamon oil in suspension in a sugary solution were deposited on the neck, shoulders and near the mouth of 11 adult rats (informants) in one colony but not in the other. In both colonies, the rats were presented with two novel food types: peppermint and cinnamon-scented wheat grain, presented in two pairs of familiar feeding boxes. Each pair of boxes thus provided the rats with a choice between the two food types (which previous experiments had shown to be equally palatable to rats). To eliminate the possibility that food selection might be caused by neophobia to a new site rather than to the new food, the

scented grain was placed in four familiar feeding boxes, previously containing non-scented wheat grain. In addition, rats could feed on non-scented grain in four other familiar feeding boxes distributed throughout the enclosure. The timing of visits to all feeding sites, as well as the identity of selected individuals within the

colony, was recorded continuously using an automatic recording system (Berdoy and Evans 1990).

Before the treatment of the informants, rats in both colonies were highly and equally neophobic to both types of scented grain (Figure 7).

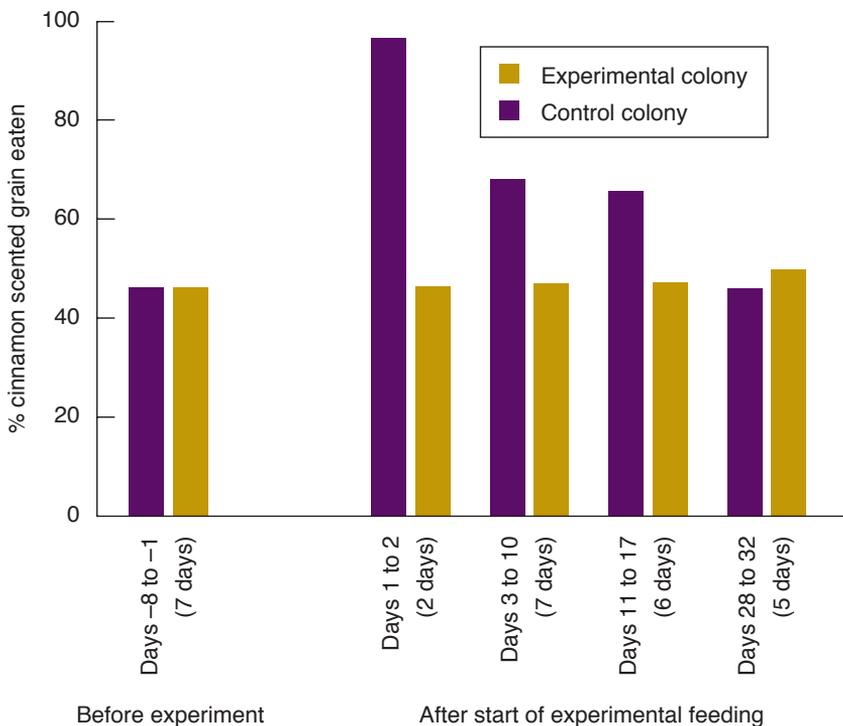


Figure 7. Change in preference for feeding sites in two colonies of wild rats, as expressed by the proportion of cinnamon-scented grain eaten. In the control colony, the introduction of cinnamon and peppermint-scented grain was associated with no change in relative use of feeding sites. However, in the experimental colony which had ‘informants’ (cinnamon-scented animals) introduced to the colony before the introduction of the scented grain, there was a preference for the cinnamon over peppermint flavoured feeds. This remained statistically significant for two weeks ($p = 0.004$, permutation test).

However, following the tainting of the informants in one colony, their companions showed a significant preference for cinnamon over peppermint, whereas no such effect was observed in the control enclosure. The informants themselves were equally reluctant to eat both types of grain at first. Subsequently, however, the informants too began to show a preference for cinnamon, perhaps as they in turn were influenced by the odours on the rats they had beguiled into eating cinnamon. It is noteworthy that, although the informants reduced neophobia towards cinnamon, nonetheless both scented grains were largely eschewed by the colonies which showed a neophobic response that was significant for at least 40 days. Indeed, some individuals avoided the scented grains completely. Furthermore, the switch to eating novel foods did not always occur gradually. For example, one dominant male, after avoiding the novel foods for the first five nights, ate the cinnamon-scented grain almost exclusively (90%) on the sixth night. This new diet selection was associated with a night of intense mating effort from the male, with no feeding during the first half of the night, and a characteristic pre-dawn peak of feeding activity.

These results draw attention to a number of other parameters which are likely to influence diet selection in the wild: neophobia, the level of information, site preference, competition and the timing of feeding (Berdoy 1994). Thus while much remains to be discovered, our experiments point to the costs and benefits of sociality in decision making. And for a mammal under such heavy poisoning pressure as the rat, these decisions are of immediate practical relevance.

RAT-BORNE DISEASE

Parasite-altered behaviour

The problems of controlling rats, many of which revolve around neophobia, might seem largely separate from their role as disease vectors. However, we have revealed an intimate link between the two, at least with regard to infection with the protozoan *Toxoplasma gondii* (Webster 1994a; Webster et al. 1994, 1995; Berdoy et al. 1995b,c; Webster and Berdoy 1997). Infection with *Toxoplasma* alters rat behaviour to increase their susceptibility to predation by domestic cats, the parasite's definitive host (Hutchison et al. 1969). These behavioural changes also incidentally increase the likelihood of poisoning. *Toxoplasma* infection of rats is widespread. In a study of English farms, we found a mean prevalence of 35% among rural rats (Webster 1994a). Earlier studies had, by contrast, indicated low prevalence levels of between 0–10% (Lainson 1957; Jackson et al. 1986). The disease is of medical and economic importance: human toxoplasmosis in the United States of America reputedly accounts for more congenital abnormalities than rubella, syphilis and herpes combined (Schmidt and Roberts 1989). In sheep, the annual loss of lambs due to the infection is an estimated 100,000 in England alone (Berverley 1976). Yet despite the importance of rats in the diet of cats, and hence the subsequent opportunities for direct and indirect transmission of *Toxoplasma* to humans, wild rats have until recently been dismissed as unimportant to the dissemination of this disease. The discovery by Webster (1994a) that the infection can be perpetuated even in the absence of cats (the final hosts) (cf.

Wallace 1981) by congenital transmission, means that rats represent an important wildlife intermediate-host reservoir for toxoplasmosis.

In evolutionary terms, a parasite's goal is to increase the chances of infective stages meeting their host species. One adaptive route to this goal is host-behaviour manipulation. An obvious way of facilitating *Toxoplasma* transmission from an infected rat to a cat is to enhance the rat's activity levels: cats are attracted to moving objects and show little interest in stationary ones (Hubel and Weisel 1962; Leyhausen 1979). A study of the activities of 140 rats revealed that those infected with *Toxoplasma* were significantly more active than uninfected rats (consistent with findings in lab mice—Hutchison et al. 1980; Hay et al. 1983a,b). This was true both for rats that had acquired *Toxoplasma* as adults and for those which had acquired it congenitally. In contrast, rats harbouring parasites with direct life cycles, such as *Cryptosporidium parvum*, did not exhibit any altered activity (Webster 1994b; Webster et al. 1994). *Toxoplasma*-infected wild rats were also generally less neophobic of novel foods (see also Stretch et al. 1960a,b) (Figure 8) and, at farmsteads where the majority of the rat population could be sampled, were trapped more quickly than uninfected rats. Furthermore, they were more curious: when one of us stood in the enclosure it turned out that rats infected with *Toxoplasma* approached more closely than non-infected animals (Berdoy et al. 1995b). We further investigated whether *Toxoplasma*-infected and non-infected rats differed in their reaction to potential predation by cats. It is widely recognised that rats, including naive

laboratory animals, show an innate avoidance of cat odour (Vernet-Maury et al. 1984; Blanchard et al. 1990; Berdoy and Macdonald 1991; Klein et al. 1994). In our outdoor enclosures, we presented adult rats with areas containing one of four distinct odours: the rat's own smell (own straw bedding), neutral smell (water), rabbit odour (rabbit urine) and cat odour (cat urine). As expected, non-infected rats showed a healthy avoidance of cat-scented areas, visiting them significantly less than other sites. However, in accordance with the manipulation hypothesis, infected rats however were significantly less averse and showed no overall avoidance of areas with signs of cat presence. A proportion even appeared to show a significant preference for the areas scented with odours of predators (M. Berdoy et al., unpublished data).

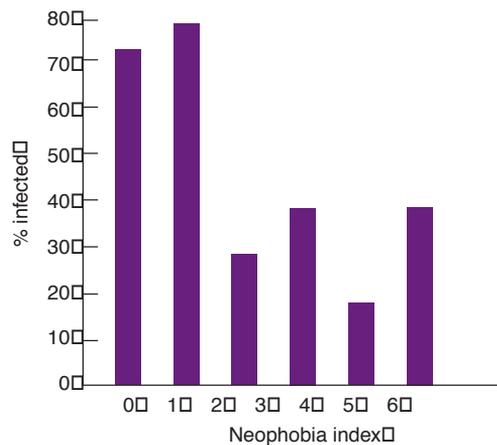


Figure 8. Prevalence of *Toxoplasma*-positive rats in each neophobia index category, where a score of 0 indicated no neophobia and 6 extreme neophobia (n = 36). The figure illustrates that infected rats were less neophobic than non-infected individuals ($F_{1,34} = 5.0, p = 0.03$).

Alterations induced by *T. gondii* infection were confined to the predator's odour, as both types of rats behaved similarly with respect to areas containing other odours. These kamikaze rats were seemingly neither debilitated nor deranged in other respects. For example, in scramble competition for mates they secured just as many copulations as did uninfected rats, and were of equal social status (Berdoy et al. 1995b) (cf. Rau 1983, 1984; Freeland 1981: infection with *Trichinella spiralis* and *Heligmosomoides polygyrus*, respectively, prevent dominance in mice). It seems, therefore, that *Toxoplasma* affects specific behavioural traits likely to make rats more susceptible to predation by the felid definitive host. According to the saying, curiosity may or may not kill the cat ...but it is likely to kill the rat!

This kamikaze tendency raises intriguing evolutionary questions. Diminished caution of infected rats, a species well known for their fearfulness of novel stimuli, could arguably enhance the likelihood of their being preyed on by cats. However, diminished neophobia also seems certain to make wild rats more prone to poisoning by man. If a poisoned rat were more easily caught by cats, the parasite would be disadvantaged if the cats then succumbed to secondary poisoning. Although comprehensive vermin control programs are a very recent development in evolutionary terms, it is reasonable to assume that they have already begun to affect the ecology of *Toxoplasma* transmission. It is also interesting to consider the antiquity of this parasite-altered behaviour; does it have its origins in the predator-prey arms race between wild felids and rats? Has the adaptation been

enhanced by the intensity of the interaction between rats and domestic cats during the last 4,000 years of shared peridomestic existence? Is the same behavioural modification found in other murine rodents?

Rural rat diseases

We investigated the prevalence of zoonoses in approximately 600 wild Norway rats captured on farms in southern England (Table 1). Thirteen zoonotic and ten non-zoonotic species of parasite were identified, many of which had never previously been recorded, or even investigated, in the United Kingdom (Webster and Macdonald 1995a). In addition to *Toxoplasma gondii*, another protozoan, *Cryptosporidium parvum*, which causes enteritis and enterocolitis in humans and other mammals (Perryman 1990) was found to be widespread (Webster and Macdonald 1995b; previously reported in Japan—Iseki 1986). The link between domestic cats and wild rats in the transmission of human disease was continued by the discovery of the rickettsian parasite, *Coxiella burnetii*, the causative agent for Q-fever (Webster et al. 1995b). Q-fever outbreaks occur sporadically (Marrie 1990a,b) and no common source has been identified. However, cases in humans are often linked with infection in domestic cats. In contrast, dogs, which occupy a similar peri-domestic niche, are rarely carriers of the parasite (Marrie et al. 1985; Baldelli et al. 1992). An obvious difference between the two, which might contribute to their radically different likelihood of acquiring *C. burnetii*, is the much more active predatory behaviour of cats.

Perhaps the most dramatic find of our surveys was the presence, for the first time in Europe, of hantavirus antibodies in wild animals (Webster and Macdonald 1995a). Hantaan viruses cause a group of illnesses in humans collectively referred to as hantaan fever or haemorrhagic fever with renal syndrome. Although a harmless, persistent infection in rodents, the disease may be extremely serious in humans. The discovery of hantavirus infection reaffirms the need to monitor the disease status of wild rats. Hantavirus transmission is strongly associated with intraspecific wounding (Glass et al. 1988). It is therefore possible that ill-planned control operations which disrupt the social hierarchy of rat groups, but fail to achieve eradication, could actually increase the prevalence of the disease (see Swinton et al. 1997). Our surveys also have demonstrated the importance of confirming rat disease status in different environments: *Leptospira* and *Salmonella* are usually considered to be highly prevalent among wild rats (e.g. Waitkins 1991; Chomel 1992), yet the former was relatively rare (14% prevalence) and the latter absent among rats studied on British farms (Webster et al. 1995a,c; see Nakashima et al. 1978). Other possible reservoirs of these diseases must therefore be investigated.

RAT CONTROL AND THE EVOLUTION OF RESISTANCE

Despite prolonged and intensive efforts to eradicate the Norway rat, the species remains a major pest. Attempts to control rat populations by poisoning tell a story of attacks and counter-attacks, currently unfolding before our eyes in a (largely

unintended) billion-pound experimental demonstration of evolution in action. Rats have two main defences against poisoning campaigns: increasingly efficient behavioural adaptations, and physiological resistance to warfarin (Boyle 1960; Greaves 1985) and now, at least incipiently, resistance to second generation anticoagulants (Greaves et al. 1982a; Gill et al. 1992).

Table 1. Prevalence of zoonoses and zoonotic agents in approximately 600 wild brown rats from farms in southern England.

Zoonoses/Zoonotic Agents	% Infected Rats
Ectoparasites	
Fleas	100
Mites	67
Lice	38
Ticks	0
Helminths	
<i>Capillaria</i> spp.	23
<i>Hymenolepis diminuta</i>	22
<i>Toxocara cati</i>	15
<i>Hymenolepis nana</i>	11
<i>Taenia taeniaeformis</i>	11
Bacteria	
<i>Leptospira</i> spp.	14
<i>Yersinia enterocolitica</i>	11
<i>Listeria</i> spp.	11
<i>Pasteurella</i> spp.	6
<i>Pseudomonas</i> spp.	4
<i>Borrelia burgdorferi</i>	0
<i>Salmonella</i> spp.	0
Protozoa	
<i>Cryptosporidium parvum</i>	63
<i>Toxoplasma gondii</i>	35
<i>Babesia</i> spp.	0
<i>Sarcocystis</i> spp.	0
Rickettsia	
<i>Coxiella burnetti</i>	34
Virus	
Hantavirus	4
Cowpox	0

Behavioural resistance

As mentioned above, many rats react to novel stimuli with extreme caution. Poison avoidance is also enhanced by their ability to associate the metabolic consequences of a food, long after it was ingested, and their capacity to interpret cues from other group members about the safety of foods. With these phenomena in mind, and observing that some rat populations were exceptionally difficult to poison (indeed they seemed not to eat the poison), the idea arose that they might have evolved enhanced behavioural resistance. A notable instance was the case of rats in Hampshire (Brunton et al. 1993, see also Greaves et al. 1982b). To confirm that the failure of anticoagulant poisons in Hampshire was not attributable to physiological resistance, we organised a control campaign with a non-anticoagulant poison, calciferol, to which there is no physiological resistance. Although some rats succumbed, at least 20–50% survived, despite repeated and intimate access to the poisoned bait. Clearly, they were not eating lethal doses. Three, not necessarily exclusive, factors might have explained this: (a) genetically enhanced neophobia; (b) experience; and (c) the stability of the environment. Our enclosure trials allowed us to discount the genetic explanation for hyper-neophobia: as discussed previously, the Hampshire rats were actually less neophobic than were survivors from a poisoning program in Wales. The evidence instead suggested that the abundant supply of alternative food, and the stable environment, were more likely explanations of the rats' reluctance to eat bait (Brunton et al. 1993). The farms in Hampshire, on which

the 'resistant' rats were found, tended to be large and surrounded by fields of cereals, and corn is often stored loose in buildings. This provides an abundant and relatively predictable alternative food supply. Rats living in this environment can therefore 'afford' to be neophobic. By contrast, in mid-Wales, where rat control by poisoning is widely held to be successful, farms tend to be smaller with more livestock and less stored grain. In these less predictable environments, rats would need to be more opportunistic.

Physiological resistance

The introduction of the anticoagulant poisons, such as warfarin, marked a breakthrough in rat control. Due to their slow action, there is a reduced likelihood of aversion learning because the animal has already ingested a lethal dose by the time the symptoms of toxicosis develop (e.g. Nachman and Hartley 1975).

Warfarin, the most commonly used rodenticide for the last thirty years, is an anticoagulant poison which affects the biogenesis of blood clotting factors, ultimately causing death by many small internal haemorrhages. The production of several blood clotting factors is driven by a series of reactions where vitamin K is cyclically oxidised and reduced (Bell and Caldwell 1973; MacNicol 1988). A simple vitamin K deficiency or substances disrupting the vitamin K cycle—such as warfarin—lead to the production of lower levels of blood clotting factors and therefore to poor coagulation and an increased risk of haemorrhage.

The prompt appearance of resistance to warfarin is a compelling example of the

power of natural selection: by 1972, less than two decades after its introduction in England, warfarin resistance was reported in 12 areas in the United Kingdom (Greaves and Rennison 1973).

The costs of physiological resistance

The new benefits enjoyed by resistant rats involve new costs. In Welsh populations, where the mechanisms of resistance have been best studied, the altered enzyme present in warfarin-resistant individuals, whilst less affected by warfarin, is also less efficient at producing vitamin K (Greaves and Ayres 1969). This results in a natural vitamin K deficiency (Hermodsen et al. 1969) and ultimately a reduced coagulating activity in resistant individuals. Resistant rats are in a constant state of vitamin K deficiency and require a greater than normal amount of vitamin K in their diet in order to retain a normal clotting activity. Homozygous resistant rats need even more dietary vitamin K than heterozygous resistant rats (Hermodsen et al. 1969; see also Greaves and Ayres 1973; Martin 1973). The costs of resistance are substantial, particularly in homozygotes, and can lead to selective deaths during the first few weeks after birth (Bishop et al. 1977). Even when sub-lethal, resistance may also affect other components of fitness such as growth, social status and reproduction (Smith et al. 1991b).

These findings are of particular theoretical and practical relevance because the fitness costs incurred by resistant animals may affect the rate of spread and maintenance of the resistance allele in wild populations. Balanced polymorphism in wild rat populations regularly controlled with warfarin suggests the existence of a

selective advantage of heterozygotes (Greaves et al. 1977). This is consistent with the interpretation that susceptible rats face reduced fitness due to the effects of the poison, and homozygous resistant rats have reduced fitness due to vitamin K deficiency. Heterozygotes, on the other hand, enjoy an efficient compromise: they are more resistant to warfarin than susceptible rats, while being less subject to vitamin K deficiency than homozygous resistant rats. In practical terms, the lower fitness of resistant genotypes (heterozygotes included) in the absence of poison (Partridge 1979) advocates a temporary relaxation of the use of warfarin to reduce the frequency of resistant individuals (Smith and Greaves 1987).

A new resistance

There may be a new strain of resistance amongst rats caught in southern England (Smith et al. 1993). We found that heterozygous resistance to warfarin poisoning was much higher than expected amongst 173 rats taken into captivity from two populations which had resisted poisoning in the wild (71% and 76% were heterozygous resistant, versus expected values of 50% and 49%; $p < 0.001$ in both cases) (Gill et al. 1992). Moreover, while warfarin-resistant rats normally have lower body weights, these animals had slightly higher than average weights (Smith et al. 1993, 1994). These results suggest that these resistant rats, instead of suffering from the expected costs of resistance, benefited from a similar if not higher fitness than the susceptible genotypes, even in the absence of poison. Apart from its theoretical interest, these results have profound management

implications. Resistance could lie dormant, if not spread, amongst rat populations living in warfarin-free environments, ready to counteract renewed poisoning efforts (Berdoy and Smith 1993). Nothing is yet known about the physiological basis of this potentially fascinating new development in the chemical arms race between humans and rats, but our results suggest that rats may currently be ahead in that race.

CONCLUSION

A full understanding of the biology of target pest species is vital to the design of effective management strategies. Nowhere, perhaps, is this better illustrated than in the case of the Norway rat, *R. norvegicus*. Not only are rats extremely widespread and adaptable, but they are also notoriously difficult to control. We have demonstrated that knowledge of the social organisation and movements of rats can assist in more effective placing of bait. Recognition of the complex feeding behaviour of rats is also of crucial importance to the success of poisoning strategies: neophobia, food preferences and aversive conditioning can all limit bait uptake. The biological approach to pest management can also reveal the need for strategies which may at first appear counter-intuitive. For example, the relaxation of poisoning pressure may actually improve the success of rat control in the long term, by reducing the frequency of resistant individuals in the population. Finally, a scientific framework will assist in the proper evaluation of the economic and public health significance of pest control operations. For example, examination of data on rat population dynamics and behaviour under

conditions of high food availability suggests that new strategies are needed to complement lethal control operations. Similarly, we have demonstrated that rats may be less important than generally thought in the transmission of certain zoonoses (for example *Salmonella* sp. and *Leptospira* sp.), but that consideration must now be given to their role in the transmission of diseases such as Q-fever.

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