The need to implement the landscape of fear within rodent pest management strategies

Running title: **Landscape of fear as rodent management strategy**

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Abstract

Current reactive pest management methods have serious drawbacks such as the heavy reliance on chemicals, emerging genetic rodenticide resistance, and high secondary exposure risks. Rodent control needs to be based on pest-species ecology and ethology to facilitate development of ecologically-based rodent management (EBRM). An important aspect of EBRM is a strong understanding of

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rodent pest species ecology, behaviour, and spatiotemporal factors. Gaining insight in the behaviour of pest-species is a key aspect of EBRM. The landscape of fear is a mapping of the spatial variation in the foraging cost arising from the risk of predation and reflects levels of fear a prey species perceives at different locations within its home range. In practice, the landscape of fear (LOF) is a mapping of habitat use as a result of perceived fear, which shows where bait or traps are most likely to be encountered and used by rodents. Several studies link perceived predation risk of foraging animals with quitting-harvest rates or giving-up densities (GUDs). GUDs have been used to reflect foraging behaviour strategies of predator avoidance, but to our knowledge very few papers have directly used GUDs in relation to pest management strategies. An opportunity for rodent control strategies lies in the integration of the LOF of rodents in EBRM methodologies. Rodent management could be more efficient and effective by concentrating on those areas where rodents perceive the least levels of predation risk.

Keywords: rodent ecology; ecologically-based rodent management; GUD; IPM; predation risk; rodent control; landscape of fear

1 INTRODUCTION

Putting integrated pest management (IPM) into practice with respect to rodents has often failed to recognise that rodent control needs to be based on a solid understanding of species-specific behaviours, biology and the phenology of damage caused by different rodent species affecting agricultural production. In the past, there has been more attention for insect pests compared to rodent pests, and especially in developing countries it is therefore often thought that the ‘I’ in IPM stands for ‘Insect’.[1] A result is that IPM strategies for rodent pests still lag seriously behind IPM strategies for insect pests. Effective rodent management in an agricultural landscape consists of four general elements: (I) prevention, (II) monitoring, (III) implementation of a combination of control methods, and (IV) community involvement in management.[1-2]

1.1. Ecologically-based rodent management

Ecologically-based rodent management (EBRM) builds on IPM; the reduction of the impact of rodent pests by using specific knowledge about rodent species behaviour, ecology, biology and damage to sustainably manage rodent pests. EBRM proceeds on the basis that integrated rodent management strategies can be developed from a sound ecological basis (e.g. rodent pest species’ habitat use and population dynamics) in order to reduce the economic and social impact of rodent pests in cost-beneficial ways that do not adversely affect the environment.[3-4] EBRM was promoted due to a growing demand for more effective and species-specific rodent control strategies that were not entirely recognised by early IPM practitioners who overly relied on chemical rodenticides.[3] Moreover, rodenticide use has become less acceptable because of increased genetic resistance[5-6] and because of heightened animal welfare concerns.[7]

Generally, traditional forms of pest management are reactive; rodent control is mostly practiced once damage to crops or stored produce becomes visible.[8] Several Asian studies have shown EBRM to be highly effective in diminishing rodent damage[9-12] and have reduced farmers' reliance on rodenticides.[10-11, 13-14] For EBRM to be effective it is also important to recognise that less than 10% of all rodent species are pest species, and many current rodent control methods do not sufficiently discriminate between pest and non-pest species.[15] Moreover, it is often not known what proportion of the population of a pest species needs to be culled for a significant reduction in economic damage.[8, 15] Thus more knowledge (i.e. monitoring) on the species present, their behaviour, and the consequences of their presence is essential for effective control.

1.2. Progression from dominance of rodenticides to integrated rodent management

In 1944, the accidental discovery of anticoagulant rodenticides occurred in the USA by accident through the detection of dicoumarin (warfarin) in spoiled sweet clover hay fed to cattle that subsequently suffered from internal bleeding.[16-17] Because rodents do not immediately feel ill after eating bait laced with warfarin, warfarin and its modern-day anticoagulant analogues have become THE definitive tool for controlling rodents. Until the late 1980s, their efficacy and relative safety certainly contributed to stifling other research avenues on rodent pest management such as developing more ecologically sound methods of rodent management.[16] Rodent control practices in agricultural environments are still mostly based on the use of rodenticides.[8, 18-20] However, incorrect application of such chemicals fast tracks the development of rodenticide resistance (reported from 1966 onwards for several rodent species) and increases the risk of both primary and exposure of predators.[21]

1.3. State of the art of EBRM use on pest rodents

An important aspect of EBRM is the use of spatio-temporal factors in the context of the population dynamics of rodent pests and the agricultural resource to be protected. As an example, it is more effective to cull far fewer animals during the early stages of rice production than to kill many later on in the season to reduce crop damage.[15] The EBRM spatio-temporal aspect is often applied in cropping systems to reduce pre-harvest losses, but there have been few studies on EBRM to reduce post-harvest losses. Fluctuations in the population abundance of peri-urban and urban rodent species (rodent species that are continuously present in the neighbourhood of humans and cause losses to stored products and increased risks of disease transmission) may be less than those of field rodent species, but the spatio-temporal aspect of EBRM is still important. For example, if rodent numbers are managed before agricultural produce is put into a storage facility, the population growth of rodent pests and negative consequences to stored grain can be significantly curtailed. Especially in the post-harvest situation, rodent management should focus more on the behaviour of the pest rodent species than on the current reactive methods. A behaviour all animals have in common is the search for provisions. So what happens when one focusses on species-specific foraging behaviour to gain more knowledge to enable managing those pest-species?

2. SEARCH FOR PROVISIONS

The optimisation of foraging behaviour of animals addressing what food type should be included in the diet was first published by Pianka and MacArthur[22] and Emlen.[23] Charnov developed in 1976 the first optimal patch use model, which is known as the Marginal Value Theorem (MVT).[24] This theorem hypothesizes that animals foraging assume that nutrition products occur in clusters, and that their food consumption decreases linearly (but not constant) with the time spent on that exact location. When making foraging decisions, animals balance the benefit of energy rewards and the price of predation.[25] The MVT predicts that animals foraging in a patch will decide whether to depart is not based on depletion of a food patch, but rather on the assessment of costs of foraging and the yield rate of the current patch versus the yield rate of another 'new' food patch.[24, 26] By creating food patches and assessing the amount of food left after foraging, the giving-up density (GUD)[36] of a food source becomes a measurable unit.[25, 27-28] The GUD reflects the perceived costs of foraging on that location. The more food left in a patch after the departure of an animal, the higher the GUD, indicating high costs.[25] GUDs provide insights into the feeding behaviour and habitat preferences of animals.[25, 29] Furthermore, GUDs also reveal the balance between food and safety; the metabolic costs of a foraging animal, its perceived predation risk during foraging, and the missed opportunity costs (MOC) of the forager by not engaging in activities other than foraging.[25, 30] With feeding rate being a direct function to food density, GUDs can be used as an index of the forager's quitting harvest rate.[31-32]

2.1 Perceived predation risks

Because rodents can serve as prey for many different species of reptiles, birds and mammals, they avoid places where the relative risk of predation is high. Both indirect cues (e.g. vegetation cover, weather conditions, light intensity) as well as direct cues (e.g. sound, odours, urine, or other excrements from potential predators) enable rodents to assess predation risk during foraging.[33] A study on the effect of owl predation on rodents' search for provisions in America showed that adjustments in foraging behaviour as a response to perceived predation risk are predominantly based on an awareness of the presence of a predator, rather than on the actual capture or killing of prey by the predator.[25{Verdolin, 2006 #162, 34] Brown[25] postulates that prey animals 'manage risk' according to H = C + P + MOC, where H is harvest rate, C the metabolic costs, and P stands for the costs of risk of predation. Research on foraging and predation risk trade-off has been used in many different animal contexts, from aquatic to terrestrial systems.[35] A review in 2013 on GUD methodologies discussed its use, practical benefits and drawbacks and gave insight into the many species that have been studied (mule deer (*Odocoileus hemionus*), red fox (*Vulpes vulpes)*, voles (*Microtus* spp. and *Myodes* spp., gerbils (*Gerbillus allenbyi*), gold fish (*Carassius auratus*), squirrels (*Tamiasciurus hudsonicus, Callospermophilus lateralis,* and *Sciurus niger*), mice (*Rhabdomys pumilio, Baeolophus bicolor, Acomys russatus, Acomys cahirinus* and *Peromyscus maniculatus*), possums (*Trichosurus vulpecula*), rats (*Rattus* *fuscipes*), chipmunks (*Tamias minimus*)).[36] For all foraging animal species, the perception of safety of feeding activities includes the encounter rate with predators, the lethality of the predator, and the chance of surviving predation.[30, 37-39] Prey animals continuously have to balance between demand for food and safety, e.g. reduced predation risk.[40] With the costs of risk of predation (P) varying across the landscape, so will the intensity of patch exploitation. The way in which animals use their habitat during their foraging behaviour[41] as a result of fear for predation is called the landscape of fear (LOF). Such a landscape is strongly based on the ecology of a particular prey species and on the ecology and hunting techniques of their predators.[3, 42] In our opinion, the LOF can be seen wider than the concept introduced by Laundré *et al*.,[41] and should include both the way foraging animals use their habitat as result of perceived fear, as well as an actual landscape. Thus besides predator-prey relations, the LOF also can be constructed on perceived fear of intra-specific relations. An intruder (e.g. rat from a different colony) will also be able to provoke fear among rats in a resident colony,[43] however, intruders can also be in fear of residents. In this case risk of injury from interference and aggression from conspecifics will affect the LOF.

3. MAKING BETTER USE OF RODENTS' NATURAL BEHAVIOUR

Several studies have linked perceived predation risk of foraging animals with their quitting harvest rates or GUDs (review by Brown and Kotler).[30] The LOF reflects levels of fear of predation perceived by a prey species on different locations within its home range.[44] The LOF is species-specific; our assumption is that a spatial LOF will look different for the grey squirrel (*Sciurus carolinensis*) than for the

Norway rat (*Rattus norvegicus)* because each species will perceive fear of predation via different cues. Furthermore, each prey-species has different aptitudes (e.g. climbing ability, speed, agility) and thus each species is vulnerable to different degrees to different predators (e.g. terrestrial or/and aerial[32]), which leads to each species having different predation costs of foraging (i.e. fear). Knowledge of a species specific short-term temporal feeding patterns (e.g. night vs. day activity) could be an effective guide for trap or bait placement and offers possibilities to reduce risks for non-target animals (e.g. by making the trap inactive during times the pest species is inactive). Knowledge on species specific behaviour could also improve trap/bait placement and trapping systems. When combining the perceived risk of predation with rodent behavioural responses, spatial use patterns of individuals could be explained.[44] In applying these concepts of rodent behaviour on rodent management, some rodent species, e.g. Norway rats (*R. norvegicus*), express a degree of neophobic behaviour, which partly explains poor bait uptake when rodenticides are applied; whilst other species, e.g. house mice, show neophilia and innate curiosity for what is new in their environment.[45-46]

3.1 Landscape of fear as a component of rodent management

A recent study examined the relationship between giving-up densities (GUDs) of *Rattus tanezumi* and the spatial heterogeneity of their damage to rice crops in the Philippines.[47] They concluded that bait or trap placement towards the centre of rice crops that are typically <0.1 ha, would be more likely to be visited by rats. Another study in wheat crops in Australia used GUDs to assess whether house mice modified their habitat selection based on perceived predation risk.[29] Both studies highlighted that a better understanding of factors influencing habitat use of rodent pests could aid decisions on their management. What is lacking is objective evidence on whether pest control strategies based on the habitat use of pest rodents are more effective and have a more long-term effect than reactive rodent management. We suggest that a better understanding of rodent behavioural ecology, especially the concept of the LOF, will result in more effective strategies for management of rodent pests. To be able to use the LOF in management, it is essential to identify the possible advantages and disadvantages, and current knowledge gaps of the LOF methodology, which can point the way for further research.

3.2. Gaps and opportunities for implementation of the LOF as rodent management tool

A classic paper by Rosenzweig[48] provides prescient advice for pest-managers to take habitat selection into account in order to improve the management results *"Pest populations may be controlled most cheaply by concentrating on their cradle habitats (although natural selection might interfere)"*[48], which is also stated years later by Morris.[49] As discussed earlier, not only habitat use plays a role when developing successful management methods, but also foraging behaviours should be taken into account as they provide reliable indicators for future situations (more reliable than use of 'old' cues indicating the past).[50] We feel that GUDs are a valuable tool to measure an animal's decision making. Research on GUDs as a monitoring tool for rodent species habitat preferences in relation to population densities and food supply indicate that rodents take greater risks when foraging during periods of high animal densities and resource depletion.[29, 51] Therefore, it is important to monitor the number of animals present; the perceived risk of an animal is lower when it lives in a large group, than when it is on its own. Moreover, competing species often create patterns in GUDs and habitat use that are convergent with predation risk.[52] For example, two competing prey species using the same food patches could lead to the same effect as avoidance of predation risk; the feeding rates of both prey species will deteriorate as the species use up resource levels in shared food patches. The decrease of harvest yields will lead to more effort in foraging in a food patch which by GUDs would be indicated as ‘safe’.[52] On the other hand, research from Australia showed that with high population densities of house mice, their spatial use became more opportunistic in some habitats where food is limited, which can also lead to a different result in the GUDs.[29] These facts indicate the need to evaluate inter-specific competition whilst measuring for predation risk behaviour of foraging animals when using GUDs.[32, 52] A low GUD indicates a ‘safe place’, which might result in overconsumption there, whereas uptake of bait in riskier places (high GUD) will be less. However, these dose rates might need to be adjusted to deal with the consumption rate in response to this LOF induced effect. This is only valid when a) there is no effect of density on GUDs; b) under-consumption does not deliver the required dose or c) over-consumption matters. Simple measures such as GUDs are generally cheap to conduct; however, Bedoya-Perez *et al.*[36] indicated seven important aspects that need careful consideration when using and interpreting GUDs: (1) the relation between costs and benefits of the forager is linear but not constant (e.g. curvilinear), (2) the forager’s physical condition, (3) more than one forager can visit a food patch simultaneously and sequentially, (4) composition of the food-patch (nutritional value of the food and properties of the substrate), (5) food patch predictability, (6) the forager's behaviours to maximize fitness and overcome costs of searching for provisions, and (7) non-target species foraging from food patches.[36] Based on these shortcomings, it can be stated that the use of GUDs to reflect foraging behaviour strategies of predator avoidance[40] cannot be assumed completely sufficient. However, it is indisputably clear the GUDs are an effective tool to map a population's LOF, which could be beneficial for pest-management by providing objective information on which to base decision making, collecting clear evidence of where rodents are more or less likely to forage and how to manipulate habitats to increase fear levels.

Current rodent management in agricultural and peri-urban habitats have made little use of the LOF as an opportunity to strengthen pest management. For example, intensity of rodenticide use and trapping could decrease significantly if an understanding of the LOF is applied in the spatial placement of such control interventions in agricultural landscapes.[47] This is particularly the case in developing countries where there have been few reports of studies on the spatial and foraging behaviour of major rodent pest species. Current rodent trapping sometimes includes parts of the LOF implicitly, for example the placement of traps along walls as it is known that most commensal rodents prefer to move alongside walls. Trapping studies on micro-habitat use have tried to reflect the concept of trap success depending on perceived predation risk. However, still the most effective placement of rodent traps inside and around buildings or within agricultural fields is generally based more on tacit knowledge of the pest controller rather than rigorous data on the behaviour of the targeted pest species in a landscape. Van der Merwe and Brown[53] visualised the LOF of the cape ground squirrel via a physical map that showed the predation costs of foraging (Figure 1a). A map of the LOF can show valleys representing relative safety, and peaks which indicate perceived danger (Figure 1b).[44] In both graphics the LOF was used as a model to visualise how fear could alter the area used by prey as it tries to reduce the risk of predation, specifically during foraging.[41, 44, 54] Within the LOF, animals will spend the most time in the valleys, where the perceived predation risk is the lowest. This information will enable rodent management to place traps on those specific perceived low fear locations, which we suggest will increase trapping rates and thus pest management success.

[Figure 1 could be placed around here]

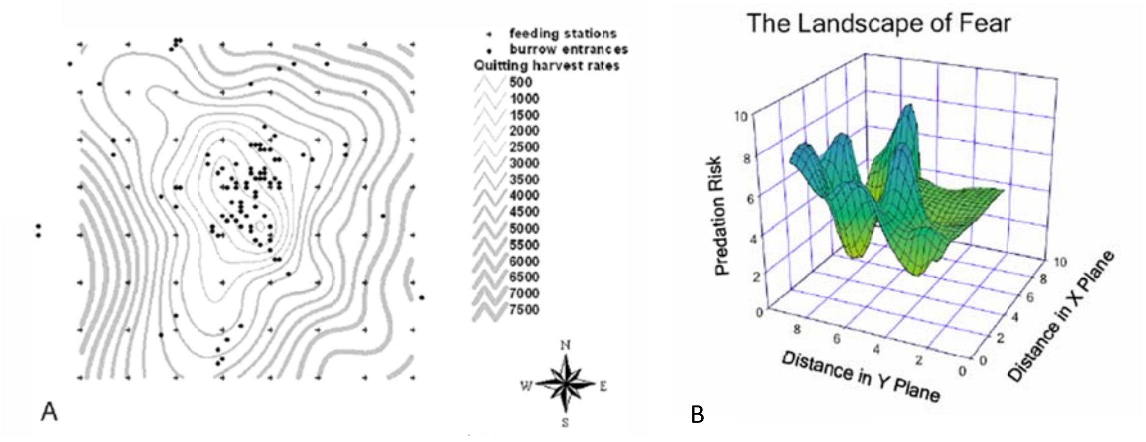

Figure 1. Two different ways of visualisation of the landscape of fear **A)** 2D map of the cape ground squirrel, the thicker the grey line, the more ‘safe’ the squirrel feels to forage (adapted from Merwe & Brown, 2008) **B)** 3D depiction of the landscape of fear, with highest giving up densities at the peaks (retrieved from Laundré et al 2010).

Rodents can alter their risk management in several ways; (I) by time allocation, e.g. shorten the exposure time and forage as fast and shortly as possible to reduce predatorily encounters, (II) by vigilance, e.g. reduce the lethality of encounters with a predator, (III) by safety in numbers by synchronised activity, and (IV) by night vs. day activity to avoid encounters with predators. Again, trapping efficiency could be substantially improved if we had mapped the LOF of the specific rodent pest species and then placed the traps accordingly (so where GUDs are lowest[47] i.e. peaks of the LOF). One option would be to conduct a systematic analysis of the behaviour of pest species where their ethology may help clarify potential actors in response to GUDs for LOF and management actions for those species. Because the LOF differs among species, it also differs between target and non-target rodents, which in turn could be used for minimising unwanted effects on non-targets. In case of doubt, the LOF of the non-target species should also be mapped to prevent trapping in overlapping perceived risk valleys. To date, however, no study has systematically mapped the spatial behaviour of rodent pest species where beneficial species would be at risk of non-target poisoning. In our view, one should concentrate on the following four key points for the use of the LOF as basis for rodent management: (I) pest species with the lowest GUD will be most easiest to target, (II) species are most susceptible during times of the year when their GUDs are lowest; during these intervals management methods will be most effective, (III) species are most likely to be trapped in (micro-) habitats where their GUDs are lowest; thus concentrate rodent management where rodents perceive the least levels of predation risk, and (IV) management strategies which increase perceived risk of predation for the target pest species will lower pest damage. Measures to promote populations of appropriate predators should be taken, such as placing out nest boxes for birds of prey (e.g. owls[28]) and educating local communities about the benefit of local biological predators (e.g. foxes[55-56]). Research into the use of “biocontrol” by domestic predators (e.g. cats, dogs) as rodent management method in Africa showed that the presence of these predators affected the foraging behaviour of pest rodents.[57] Presence of both cats and dogs increased levels of fear (measured by increased GUDs) for local foraging rodent species, which led to diminished rodent activity.[57] However, reliable scientific evidence that bio-control via predation minimizes rodent population size below damage threshold levels is not yet available.

4 CONCLUSION

Connecting the LOF to rodent pest species is a novel approach with many opportunities to further enhance ecologically-based rodent pest management. Implementing the LOF into rodent management may enable the development of preventive control rather than reactive methods through better timing and habitat targeting for trapping or placement of rodenticides. It is extremely important to continuously look at alternatives for pest-management. A recent study of Mul et al.[58] developed a fully automated pest monitoring tool to implement IPM effectively. This was done by focussing on the behaviour of the pest species, after which monitoring was conducted to develop a model which predicts the location and grow of the population.[58-59] In conclusion, for effective management, it is essential to align management methods with the pest-species biology and behaviour. Until now, there are few studies on the behaviour of commensal and non-commensal pest species over different habitats and environments (e.g. city vs countryside) which are a necessity for composing and using the LOF. It would be best to have an overview of all species present, and whether and when they compete with each other or not. The idea to use the LOF as an EBRM tool holds promise for novel strategies and capacities for practical use as a unifying behavioural ecological concept. A study on the influence of domestic predators on pest rodent foraging behaviour by Mahlaba *et al.*[57] suggest that the integration of the LOF into EBRM will provide stronger insights into the ecology of rodent pest species. The use of LOF is much stronger and broader applicable than the use of tacit knowledge, as tacit knowledge generally based on experience and can be highly subjective, and is difficult to transfer to another person by formal means The LOF concept is meant to provide a more evidence-based approach. In turn, this would enable the development of more efficient rodent management methods.

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REFERENCES

1. Singleton GR. Integrated management of rodents: a southeast Asian and Australian perspective. *Belgian Journal of Zoology*. 1997;**127**(Supplement 1):157-69.
2. Meerburg B, Bonde M, Brom F, Endepols S, Jensen A, Leirs H, et al. Towards sustainable management of rodents in organic animal husbandry. *NJAS-Wageningen Journal of Life Sciences*. 2004;**52**(2):195-205.
3. Singleton GR, Leirs H, Hinds LA, Zhang Z. Ecologically-based management of rodent pests–re-evaluating our approach to an old problem. *Ecologically-based Management of Rodent Pests Australian Centre for International Agricultural Research (ACIAR), Canberra*. 1999:17-29.
4. Smith RF, van den Bosch R. Integrated control. Kilgore WW, Doutt RL, editors1967.
5. Rost S, Pelz H-J, Menzel S, MacNicoll AD, León V, Song K-J, et al. Novel mutations in the VKORC1 gene of wild rats and mice–a response to 50 years of selection pressure by warfarin? *Bmc Genetics*. 2009;**10**(1):4.
6. Meerburg BG, van Gent-Pelzer MP, Schoelitsz B, van der Lee TA. Distribution of anticoagulant rodenticide resistance in Rattus norvegicus in the Netherlands according to Vkorc1 mutations. *Pest management science*. 2014;**70**(11):1761-6.
7. Meerburg BG, Brom FW, Kijlstra A. The ethics of rodent control. *Pest management science*. 2008;**64**(12):1205-11.
8. John A. Rodent outbreaks and rice pre-harvest losses in Southeast Asia. *Food Security*. 2014;**6**(2):249-60.
9. Singleton GR, Brown PR. Comparison of different sizes of physical barriers for controlling the impact of the rice field rat, Rattus argentiventer, in rice crops in Indonesia. *Crop Protection*. 2003;**22**(1):7-13.
10. Singleton GR, Sudarmaji, Jacob J, Krebs CJ. Integrated management to reduce rodent damage to lowland rice crops in Indonesia. *Agriculture, Ecosystems & Environment*. 2005;**107**(1):75-82.
11. Palis FG, Singleton GR, Brown PR, Huan NH, Umali C, Nga NTD. Can humans outsmart rodents? Learning to work collectively and strategically. *Wildlife Research*. 2011;**38**(7):568-78.
12. Jacob J, Singleton GR, Herawati NA, Brown PR. Ecologically based management of rodents in lowland irrigated rice fields in Indonesia. *Wildlife Research*. 2010;**37**(5):418-27.
13. Brown PR, Tuan NP, Singleton GR, Ha PTT, Hoa PT, Hue DT, et al. Ecologically based management of rodents in the real world: applied to a mixed agroecosystem in Vietnam. *Ecological Applications*. 2006;**16**(5):2000-10.
14. Brown PR, Khamphoukeo K. Changes in farmers' knowledge, attitudes and practices after implementation of ecologically-based rodent management in the uplands of Lao PDR. *Crop Protection*. 2010;**29**(6):577-82.
15. Singleton GR, Brown PR, Jacob J, Aplin KP. Unwanted and unintended effects of culling: A case for ecologically-based rodent management. *Integrative zoology*. 2007;**2**(4):247-59.
16. Hadler MR, Buckle AP. Forty five years of anticoagulant rodenticides—past, present and future trends. 1992.
17. Link KP. The anticoagulant from spoiled sweet clover hay1944.
18. Arora K, Srivastava J, Pandey G. Evaluation of racumin (coumatetralyl) based anticoagulant against the black rat, Rattus rattus Linn. *Pesticides 18 (12)*. 1984:25-7.
19. Mathur R, Prakash I. Reduction in population of Indian desert rodents with anticoagulant rodenticides. *Proceedings: Animal Sciences*. 1984;**93**(6):585-9.
20. Parshad V, Malhi C. Comparative efficacy of two methods of delivering an anticoagulant rodenticide to three species of South Asian rodents. *International biodeterioration & biodegradation*. 1995;**36**(1):89-102.
21. Jackson WB, Kaukeinen D. Resistance of Wild Norway Rats in North Carolina to Warfarin Rodenticide. *Science*. 1972;**176**(4041):1343-4.

22. MacArthur R, Pianka E. On Optimal Use of a Patchy Environment. . *The American Naturalist*. 1966;**100**(916):603-9.
23. Emlen JM. The role of time and energy in food preference. . *The American Naturalist*. 1966;**100**(916):611-7.
24. Charnov EL. Optimal foraging, the marginal value theorem. *Theoretical population biology*. 1976;**9**(2):129-36.
25. Brown JS. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology*. 1988;**22**(1):37-47.
26. Milinski M, Heller R. Influence of a predator on the optimal foraging behaviour of sticklebacks (Gasterosteus aculeatus L.). 1978.
27. Brown JS, Kotler BP, Mitchell WA. Competition between birds and mammals: a comparison of giving-up densities between crested larks and gerbils. *Evolutionary Ecology*. 1997;**11**(6):757-71.
28. Brown JS, Kotler BP, Smith RJ, Wirtz II WO. The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia*. 1988;**76**(3):408-15.
29. Ylönen H, Jacob J, Davies MJ, Singleton GR. Predation risk and habitat selection of Australian house mice , Mus domesticus, during an incipient plague: desperate behaviour due to food depletion. *Oikos*. 2002;**99**(2):284-9.
30. Brown JS, Kotler BP. Hazardous duty pay and the foraging cost of predation. *Ecology letters*. 2004;**7**(10):999-1014.
31. Schmidt KA, Brown JS, Morgan RA. Plant defenses as complementary resources: a test with squirrels. *Oikos*. 1998:130-42.
32. Makin DF, Payne HF, Kerley GI, Shrader AM. Foraging in a 3-D world: how does predation risk affect space use of vervet monkeys? *Journal of Mammalogy*. 2012;**93**(2):422-8.
33. Orrock JL, Danielson BJ, Brinkerhoff R. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. *Behavioral Ecology*. 2004;**15**(3):433-7.
34. Verdolin JL. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behavioral Ecology and Sociobiology*. 2006;**60**(4):457-64.
35. Werner EE, Hall DJ. Ontogenetic Habitat Shifts in Bluegill: The Foraging Rate-Predation Risk Trade-off. *Ecology*. 1988;**69**(5):1352-66.
36. Bedoya-Perez MA, Carthey AJR, Mella VSA, McArthur C, Banks PB. A practical guide to avoid giving up on giving-up densities. *Behavioral Ecology and Sociobiology*. 2013;**67**(10):1541-53.
37. Brown JS. Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary ecology research*. 1999;**1**(1):49-71.
38. Lima SL, Dill LM. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*. 1990;**68**(4):619-40.
39. Abrams PA. Optimal traits when there are several costs: the interaction of mortality and energy costs in determining foraging behavior. *Behavioral Ecology*. 1993;**4**(3):246-59.
40. Jacob J, Brown JS. Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. *Oikos*. 2000;**91**(1):131-8.
41. Laundré JW, Hernández L, Altendorf KB. Wolves, elk, and bison: reestablishing the" landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology*. 2001;**79**(8):1401-9.
42. Matassa CM, Trussell GC. Landscape of fear influences the relative importance of consumptive and nonconsumptive predator effects. *Ecology*. 2011;**92**(12):2258-66.
43. Davis DE, Emlen JT, Stokes AWCFpdA. Studies on Home Range in the Brown Rat. *Journal of Mammalogy*. 1948;**29**(3):207-25.
44. Laundré JW, Hernández L, Ripple WJ. The landscape of fear: ecological implications of being afraid. *Open Ecology Journal*. 2010;**3**:1-7.
45. Macdonald DW, Mathews F, Berdoy M. The behaviour and ecology of Rattus norvegicus: from opportunism to kamikaze tendencies. *Singleton, G; Hinds, L; Leirs, H*. 1999:49-80.
46. Cowan P. Neophobia and neophilia: new-object and new-place reactions of three Rattus species. *Journal of Comparative and Physiological Psychology*. 1977;**91**(1):63.

47. Jones CR, Lorica M, Renee P, Villegas JM, Ramal AF, Horgan FG, et al. The stadium effect: rodent damage patterns in rice fields explored using giving-up densities. *Integrative Zoology*. 2016.
48. Rosenzweig ML. Density-Dependent Habitat Selection: A Tool for More Effective Population Management. In: Vincent TL, Cohen Y, Grantham WJ, Kirkwood GP, Skowronski JM, editors. *Modeling and Management of Resources under Uncertainty: Proceedings of the Second US-Australia Workshop on Renewable Resource Management held at the East-West Center, Honolulu, Hawaii, December 9–12, 1985*. Berlin, Heidelberg: Springer Berlin Heidelberg; 1987. p. 98-111.
49. Morris DW. How can we apply theories of habitat selection to wildlife conservation and management? *Wildlife Research*. 2003;**30**(4):303-19.
50. Kotler BP, Morris DW, Brown JS. Direct behavioral indicators as a conservation and management tool. *Conservation Behavior: Applying Behavioral Ecology to Wildlife Conservation and Management*. 2016;**21**:307.
51. Strauß A, Solmsdorff KY, Pech R, Jacob J. Rats on the run: removal of alien terrestrial predators affects bush rat behaviour. *Behavioral Ecology and Sociobiology*. 2008;**62**(10):1551-8.
52. Morris DW. Apparent predation risk: tests of habitat selection theory reveal unexpected effects of competition. *Evolutionary Ecology Research*. 2009;**11**(2):209-25.
53. van der Merwe M, Brown JS. Mapping the landscape of fear of the cape ground squirrel (Xerus inauris). *Journal of Mammalogy*. 2008;**89**(5):1162-9.
54. Altendorf KB, Laundré JW, López González CA, Brown JS. Assessing effects of predation risk on foraging behavior of mule deer. *Journal of Mammalogy*. 2001;**82**(2):430-9.
55. Saunders G, Coman B, Kinnear J, Braysher M. Managing vertebrate pests: foxes: Australian Government Publ. Service; 1995.
56. Lindström ER, Andrén H, Angelstam P, Cederlund G, Hörnfeldt B, Jäderberg L, et al. Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. *Ecology*. 1994;**75**(4):1042-9.
57. Mahlabla TaA, Monadjem A, McCleery R, Belmain SR. Domestic cats and dogs create a landscape of fear for pest rodents around rural homesteads. *PloS one*. 2017;**12**(2):e0171593.
58. Mul MF, Ploegaert JPM, George DR, Meerburg BG, Dicke M, Groot Koerkamp PWG. Structured design of an automated monitoring tool for pest species. *Biosystems Engineering*. 2016;**151**:126-40.
59. Mul MF, Riel JWv, Roy L, Zoons J, André G, George DR, et al. Development of a model to forecast population dynamics of *Dermanyssus gallinae* in laying hen houses to facilitate Integrated Pest Management. in press.