Pest Management Science ○ SCI

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

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

2 **strategies**

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

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1   **Abstract**

2   Current reactive pest management methods have serious drawbacks such as the

3   heavy reliance on chemicals, emerging genetic rodenticide resistance, and high

4   secondary exposure risks. Rodent control needs to be based on pest-species

5   ecology and ethology to facilitate development of ecologically-based rodent

6   management (EBRM). An important aspect of EBRM is a strong understanding of

7   rodent pest species ecology, behaviour, and spatiotemporal factors. Gaining

8   insight in the behaviour of pest-species is a key aspect of EBRM. The landscape

9   of fear is a mapping of the spatial variation in the foraging cost arising from the risk

10   of predation and reflects levels of fear a prey species perceives at different

11   locations within its home range. In practice, the landscape of fear (LOF) is a

12   mapping of habitat use as a result of perceived fear, which shows where bait or

13   traps are most likely to be encountered and used by rodents. Several studies link

14   perceived predation risk of foraging animals with quitting-harvest rates or giving-up

15   densities (GUDs). GUDs have been used to reflect foraging behaviour strategies

16   of predator avoidance, but to our knowledge very few papers have directly used

17   GUDs in relation to pest management strategies. An opportunity for rodent control

18   strategies lies in the integration of the LOF of rodents in EBRM methodologies.

19   Rodent management could be more efficient and effective by concentrating on

20   those areas where rodents perceive the least levels of predation risk.

21   **Keywords:** rodent ecology; ecologically-based rodent management; GUD; IPM;

22   predation risk; rodent control; landscape of fear

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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,

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1   rodenticide use has become less acceptable because of increased genetic

2   resistance[5-6] and because of heightened animal welfare concerns.[7]

3   Generally, traditional forms of pest management are reactive; rodent control is

4   mostly practiced once damage to crops or stored produce becomes visible.[8]

5   Several Asian studies have shown EBRM to be highly effective in diminishing

6   rodent damage[9-12] and have reduced farmers' reliance on rodenticides.[10-11, 13-14]

7   For EBRM to be effective it is also important to recognise that less than 10% of all

8   rodent species are pest species, and many current rodent control methods do not

9   sufficiently discriminate between pest and non-pest species.[15] Moreover, it is

10   often not known what proportion of the population of a pest species needs to be

11   culled for a significant reduction in economic damage.[8, 15] Thus more knowledge

12   (i.e. monitoring) on the species present, their behaviour, and the consequences of

13   their presence is essential for effective control.

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1.2. Progression from dominance of rodenticides to integrated rodent management

17   In 1944, the accidental discovery of anticoagulant rodenticides occurred in the

18   USA by accident through the detection of dicoumarin (warfarin) in spoiled sweet

19   clover hay fed to cattle that subsequently suffered from internal bleeding.[16-17]

20   Because rodents do not immediately feel ill after eating bait laced with warfarin,

21   warfarin and its modern-day anticoagulant analogues have become THE definitive

22   tool for controlling rodents. Until the late 1980s, their efficacy and relative safety

23   certainly contributed to stifling other research avenues on rodent pest

24   management such as developing more ecologically sound methods of rodent

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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

1   foraging behaviour to gain more knowledge to enable managing those pest-

2   species?

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4   **2. SEARCH FOR PROVISIONS**

5   The optimisation of foraging behaviour of animals addressing what food type

6   should be included in the diet was first published by Pianka and MacArthur[22] and

7   Emlen.[23] Charnov developed in 1976 the first optimal patch use model, which is

8   known as the Marginal Value Theorem (MVT).[24] This theorem hypothesizes that

9   animals foraging assume that nutrition products occur in clusters, and that their

10 food consumption decreases linearly (but not constant) with the time spent on that

11 exact location. When making foraging decisions, animals balance the benefit of

12 energy rewards and the price of predation.[25] The MVT predicts that animals

13 foraging in a patch will decide whether to depart is not based on depletion of a

14 food patch, but rather on the assessment of costs of foraging and the yield rate of

15 the current patch versus the yield rate of another 'new' food patch.[24, 26] By

16 creating food patches and assessing the amount of food left after foraging, the

17 giving-up density (GUD)[36] of a food source becomes a measurable unit.[25, 27-28]

18 The GUD reflects the perceived costs of foraging on that location. The more food

19 left in a patch after the departure of an animal, the higher the GUD, indicating high

20 costs.[25] GUDs provide insights into the feeding behaviour and habitat preferences

21 of animals.[25, 29] Furthermore, GUDs also reveal the balance between food and

22 safety; the metabolic costs of a foraging animal, its perceived predation risk

23 during foraging, and the missed opportunity costs (MOC) of the forager by not

24 engaging in activities other than foraging.[25, 30] With feeding rate being a direct

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3 1   function to food density, GUDs can be used as an index of the forager's quitting
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5 2   harvest rate.[31-32]
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11 4   **2.1 Perceived predation risks**
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14 5   Because rodents can serve as prey for many different species of reptiles, birds
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16 6   and mammals, they avoid places where the relative risk of predation is high. Both
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18 7   indirect cues (e.g. vegetation cover, weather conditions, light intensity) as well as
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20 8   direct cues (e.g. sound, odours, urine, or other excrements from potential
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22 9   predators) enable rodents to assess predation risk during foraging.[33] A study on
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24 10   the effect of owl predation on rodents' search for provisions in America showed
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26 11   that adjustments in foraging behaviour as a response to perceived predation risk
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28 12   are predominantly based on an awareness of the presence of a predator, rather
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30 13   than on the actual capture or killing of prey by the predator.[25]{Verdolin, 2006 #162, 34}
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32 14   Brown[25] postulates that prey animals 'manage risk' according to H = C + P +
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34 15   MOC, where H is harvest rate, C the metabolic costs, and P stands for the costs
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36 16   of risk of predation. Research on foraging and predation risk trade-off has been
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38 17   used in many different animal contexts, from aquatic to terrestrial systems.[35] A
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40 18   review in 2013 on GUD methodologies discussed its use, practical benefits and
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42 19   drawbacks and gave insight into the many species that have been studied (mule
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44 20   deer (*Odocoileus hemionus*), red fox (*Vulpes vulpes)*, voles (*Microtus* spp. and
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46 21   *Myodes* spp., gerbils (*Gerbillus allenbyi*), gold fish (*Carassius auratus*), squirrels
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48 22   (*Tamiasciurus hudsonicus, Callospermophilus lateralis,* and *Sciurus niger*), mice
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50 23   (*Rhabdomys pumilio, Baeolophus bicolor, Acomys russatus, Acomys cahirinus*
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52 24   and *Peromyscus maniculatus*), possums (*Trichosurus vulpecula*), rats (*Rattus*

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1   *fuscipes*), chipmunks (*Tamias minimus*)).[36] For all foraging animal species, the

2   perception of safety of feeding activities includes the encounter rate with

3   predators, the lethality of the predator, and the chance of surviving predation.[30, 37-

4   39] Prey animals continuously have to balance between demand for food and

5   safety, e.g. reduced predation risk.[40] With the costs of risk of predation (P) varying

6   across the landscape, so will the intensity of patch exploitation. The way in which

7   animals use their habitat during their foraging behaviour[41] as a result of fear for

8   predation is called the landscape of fear (LOF). Such a landscape is strongly

9   based on the ecology of a particular prey species and on the ecology and hunting

10 techniques of their predators.[3, 42] In our opinion, the LOF can be seen wider than

11 the concept introduced by Laundré *et al.*,[41] and should include both the way

12 foraging animals use their habitat as result of perceived fear, as well as an actual

13 landscape. Thus besides predator-prey relations, the LOF also can be

14 constructed on perceived fear of intra-specific relations. An intruder (e.g. rat from

15 a different colony) will also be able to provoke fear among rats in a resident

16 colony,[43] however, intruders can also be in fear of residents. In this case risk of

17 injury from interference and aggression from conspecifics will affect the LOF.

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19 3. **MAKING BETTER USE OF RODENTS' NATURAL BEHAVIOUR**

20 Several studies have linked perceived predation risk of foraging animals with their

21 quitting harvest rates or GUDs (review by Brown and Kotler).[30] The LOF reflects

22 levels of fear of predation perceived by a prey species on different locations within

23 its home range.[44] The LOF is species-specific; our assumption is that a spatial

24 LOF will look different for the grey squirrel (*Sciurus carolinensis*) than for the

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1 Norway rat (*Rattus norvegicus)* because each species will perceive fear of

2 predation via different cues. Furthermore, each prey-species has different

3 aptitudes (e.g. climbing ability, speed, agility) and thus each species is vulnerable

4 to different degrees to different predators (e.g. terrestrial or/and aerial[32]), which

5 leads to each species having different predation costs of foraging (i.e. fear).

6 Knowledge of a species specific short-term temporal feeding patterns (e.g. night

7 vs. day activity) could be an effective guide for trap or bait placement and offers

8 possibilities to reduce risks for non-target animals (e.g. by making the trap

9 inactive during times the pest species is inactive). Knowledge on species specific

10 behaviour could also improve trap/bait placement and trapping systems. When

11 combining the perceived risk of predation with rodent behavioural responses,

12 spatial use patterns of individuals could be explained.[44] In applying these

13 concepts of rodent behaviour on rodent management, some rodent species, e.g.

14 Norway rats (*R. norvegicus*), express a degree of neophobic behaviour, which

15 partly explains poor bait uptake when rodenticides are applied; whilst other

16 species, e.g. house mice, show neophilia and innate curiosity for what is new in

17 their environment.[45-46]

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3.1 Landscape of fear as a component of rodent management

20 A recent study examined the relationship between giving-up densities (GUDs) of

21 *Rattus tanezumi* and the spatial heterogeneity of their damage to rice crops in the

22 Philippines.[47] They concluded that bait or trap placement towards the centre of

23 rice crops that are typically <0.1 ha, would be more likely to be visited by rats.

24 Another study in wheat crops in Australia used GUDs to assess whether house

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1   mice modified their habitat selection based on perceived predation risk.[29] Both

2   studies highlighted that a better understanding of factors influencing habitat use of

3   rodent pests could aid decisions on their management. What is lacking is

4   objective evidence on whether pest control strategies based on the habitat use of

5   pest rodents are more effective and have a more long-term effect than reactive

6   rodent management. We suggest that a better understanding of rodent

7   behavioural ecology, especially the concept of the LOF, will result in more

8   effective strategies for management of rodent pests. To be able to use the LOF in

9   management, it is essential to identify the possible advantages and

10   disadvantages, and current knowledge gaps of the LOF methodology, which can

11   point the way for further research.

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

15   A classic paper by Rosenzweig[48] provides prescient advice for pest-managers to

16   take habitat selection into account in order to improve the management results

17   *"Pest populations may be controlled most cheaply by concentrating on their cradle*

18   *habitats (although natural selection might interfere)"[48]*, which is also stated years

19   later by Morris.[49] As discussed earlier, not only habitat use plays a role when

20   developing successful management methods, but also foraging behaviours

21   should be taken into account as they provide reliable indicators for future

22   situations (more reliable than use of 'old' cues indicating the past).[50] We feel that

23   GUDs are a valuable tool to measure an animal's decision making. Research on

24   GUDs as a monitoring tool for rodent species habitat preferences in relation to

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1   population densities and food supply indicate that rodents take greater risks when

2   foraging during periods of high animal densities and resource depletion.[29, 51]

3   Therefore, it is important to monitor the number of animals present; the perceived

4   risk of an animal is lower when it lives in a large group, than when it is on its own.

5   Moreover, competing species often create patterns in GUDs and habitat use that

6   are convergent with predation risk.[52] For example, two competing prey species

7   using the same food patches could lead to the same effect as avoidance of

8   predation risk; the feeding rates of both prey species will deteriorate as the

9   species use up resource levels in shared food patches. The decrease of harvest

10   yields will lead to more effort in foraging in a food patch which by GUDs would be

11   indicated as 'safe'.[52] On the other hand, research from Australia showed that with

12   high population densities of house mice, their spatial use became more

13   opportunistic in some habitats where food is limited, which can also lead to a

14   different result in the GUDs.[29] These facts indicate the need to evaluate inter-

15   specific competition whilst measuring for predation risk behaviour of foraging

16   animals when using GUDs.[32, 52] A low GUD indicates a 'safe place', which might

17   result in overconsumption there, whereas uptake of bait in riskier places (high

18   GUD) will be less. However, these dose rates might need to be adjusted to deal

19   with the consumption rate in response to this LOF induced effect. This is only

20   valid when a) there is no effect of density on GUDs; b) under-consumption does

21   not deliver the required dose or c) over-consumption matters. Simple measures

22   such as GUDs are generally cheap to conduct; however, Bedoya-Perez et al.[36]

23   indicated seven important aspects that need careful consideration when using

24   and interpreting GUDs: (1) the relation between costs and benefits of the forager

25   is linear but not constant (e.g. curvilinear), (2) the forager's physical condition, (3)

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1 more than one forager can visit a food patch simultaneously and sequentially, (4)

2 composition of the food-patch (nutritional value of the food and properties of the

3 substrate), (5) food patch predictability, (6) the forager's behaviours to maximize

4 fitness and overcome costs of searching for provisions, and (7) non-target species

5 foraging from food patches.[36] Based on these shortcomings, it can be stated that

6 the use of GUDs to reflect foraging behaviour strategies of predator avoidance[40]

7 cannot be assumed completely sufficient. However, it is indisputably clear the

8 GUDs are an effective tool to map a population's LOF, which could be beneficial

9 for pest-management by providing objective information on which to base

10 decision making, collecting clear evidence of where rodents are more or less

11 likely to forage and how to manipulate habitats to increase fear levels.

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13 Current rodent management in agricultural and peri-urban habitats have made

14 little use of the LOF as an opportunity to strengthen pest management. For

15 example, intensity of rodenticide use and trapping could decrease significantly if

16 an understanding of the LOF is applied in the spatial placement of such control

17 interventions in agricultural landscapes.[47] This is particularly the case in

18 developing countries where there have been few reports of studies on the spatial

19 and foraging behaviour of major rodent pest species. Current rodent trapping

20 sometimes includes parts of the LOF implicitly, for example the placement of traps

21 along walls as it is known that most commensal rodents prefer to move alongside

22 walls. Trapping studies on micro-habitat use have tried to reflect the concept of

23 trap success depending on perceived predation risk. However, still the most

24 effective placement of rodent traps inside and around buildings or within

25 agricultural fields is generally based more on tacit knowledge of the pest controller

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3   1   rather than rigorous data on the behaviour of the targeted pest species in a
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5   2   landscape. Van der Merwe and Brown[53] visualised the LOF of the cape ground
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7   3   squirrel via a physical map that showed the predation costs of foraging (Figure
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9   4   1a). A map of the LOF can show valleys representing relative safety, and peaks
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11   5   which indicate perceived danger (Figure 1b).[44] In both graphics the LOF was used
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13   6   as a model to visualise how fear could alter the area used by prey as it tries to
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15   7   reduce the risk of predation, specifically during foraging.[41, 44, 54] Within the LOF,
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17   8   animals will spend the most time in the valleys, where the perceived predation risk
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19   9   is the lowest. This information will enable rodent management to place traps on
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21   10   those specific perceived low fear locations, which we suggest will increase
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23   11   trapping rates and thus pest management success.
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26   12   **[Figure 1 could be placed around here]**
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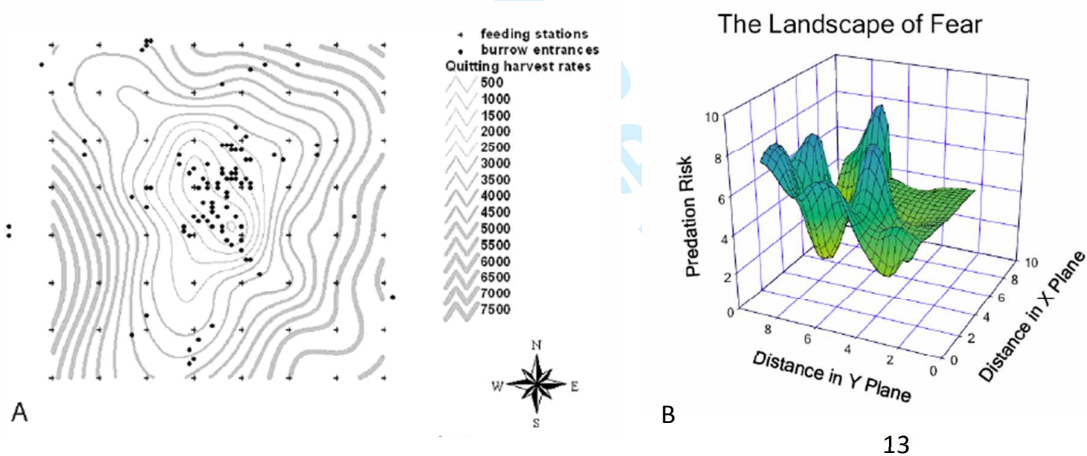28
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46   14   Figure 1. Two different ways of visualisation of the landscape of fear **A)** 2D map of the cape
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48   15   ground squirrel, the thicker the grey line, the more 'safe' the squirrel feels to forage (adapted from
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50   16   Merwe & Brown, 2008) **B)** 3D depiction of the landscape of fear, with highest giving up densities at
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52   17   the peaks (retrieved from Laundré et al 2010).
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1   Rodents can alter their risk management in several ways; (I) by time allocation,

2   e.g. shorten the exposure time and forage as fast and shortly as possible to

3   reduce predatorily encounters, (II) by vigilance, e.g. reduce the lethality of

4   encounters with a predator, (III) by safety in numbers by synchronised activity,

5   and (IV) by night vs. day activity to avoid encounters with predators. Again,

6   trapping efficiency could be substantially improved if we had mapped the LOF of

7   the specific rodent pest species and then placed the traps accordingly (so where

8   GUDs are lowest[47] i.e. peaks of the LOF). One option would be to conduct a

9   systematic analysis of the behaviour of pest species where their ethology may

10   help clarify potential actors in response to GUDs for LOF and management

11   actions for those species. Because the LOF differs among species, it also differs

12   between target and non-target rodents, which in turn could be used for minimising

13   unwanted effects on non-targets. In case of doubt, the LOF of the non-target

14   species should also be mapped to prevent trapping in overlapping perceived risk

15   valleys. To date, however, no study has systematically mapped the spatial

16   behaviour of rodent pest species where beneficial species would be at risk of non-

17   target poisoning. In our view, one should concentrate on the following four key

18   points for the use of the LOF as basis for rodent management: (I) pest species

19   with the lowest GUD will be most easiest to target, (II) species are most

20   susceptible during times of the year when their GUDs are lowest; during these

21   intervals management methods will be most effective, (III) species are most likely

22   to be trapped in (micro-) habitats where their GUDs are lowest; thus concentrate

23   rodent management where rodents perceive the least levels of predation risk, and

24   (IV) management strategies which increase perceived risk of predation for the

25   target pest species will lower pest damage. Measures to promote populations of

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1 appropriate predators should be taken, such as placing out nest boxes for birds of

2 prey (e.g. owls[28]) and educating local communities about the benefit of local

3 biological predators (e.g. foxes[55-56]). Research into the use of "biocontrol" by

4 domestic predators (e.g. cats, dogs) as rodent management method in Africa

5 showed that the presence of these predators affected the foraging behaviour of

6 pest rodents.[57] Presence of both cats and dogs increased levels of fear

7 (measured by increased GUDs) for local foraging rodent species, which led to

8 diminished rodent activity.[57] However, reliable scientific evidence that bio-control

9 via predation minimizes rodent population size below damage threshold levels is

10 not yet available.

11

4   CONCLUSION

13 Connecting the LOF to rodent pest species is a novel approach with many

14 opportunities to further enhance ecologically-based rodent pest management.

15 Implementing the LOF into rodent management may enable the development of

16 preventive control rather than reactive methods through better timing and habitat

17 targeting for trapping or placement of rodenticides. It is extremely important to

18 continuously look at alternatives for pest-management. A recent study of Mul et

19 al.[58] developed a fully automated pest monitoring tool to implement IPM

20 effectively. This was done by focussing on the behaviour of the pest species, after

21 which monitoring was conducted to develop a model which predicts the location

22 and grow of the population.[58-59] In conclusion, for effective management, it is

23 essential to align management methods with the pest-species biology and

24 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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1 **The need to implement the landscape of fear within rodent pest management**

2 **strategies**

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

4

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Abstract

~~BACKGROUND:~~ Current reactive pest management methods have serious drawbacks such as the heavy reliance on chemicals, emerging <u>genetic</u> rodenticide resistance, and high secondary ~~poisoning~~<u>exposure</u> risks. Rodent control needs to be based on pest-species ecology and ethology to facilitate development of ecologically-based rodent management (EBRM). ~~RESULTS: The need for EBRM is increasing due to less effectiveness of rodenticide use through genetic resistance and because of animal welfare concerns.~~ An important aspect of EBRM is a strong understanding of rodent pest species ecology, behaviour, and spatiotemporal factors. ~~Several studies link perceived predation risk of foraging animals with quitting-harvest rates or giving-up densities (GUDs).~~ 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. <u>Several studies link perceived predation risk of foraging animals with quitting-harvest rates or giving-up densities (GUDs).</u> ~~CONCLUSION:~~ 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.

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3

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, ~~breeding rates~~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. Originally, IPM was developed to promote pest management methods with the smallest interruptive effect to other ecological systems.[2] An important aspect of IPM is the integration of multiple management methods in order to provide more effective pest management than when these practices are carried out separately. Translation of IPM programmes for insect pests to rodent pest methodologies could increase the effectiveness of IPM of rodent pests.[1] 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, 3]~~ 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

4

Ecologically-based rodent management (EBRM) ~~is a term popularised after a workshop in 1996 in Tanzania with the goal to re-emphasize the importance of 'know your enemy' in developing integrated rodent management solutions. The aim of EBRM is similar to~~builds on IPM; the reduction of the impact of rodent pests by using specific knowledge about rodent species behaviour, ecology, ~~physiology~~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.[2, 4][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.[4][3] Moreover, rodenticide use has become less acceptable because of increased genetic resistance[5-6] and because of heightened animal welfare concerns.[7] ~~We discuss more on rodenticide resistance in the next section.~~

Generally, traditional forms of pest management are reactive; rodent control is mostly practiced once damage to crops or stored produce becomes visible.[8] ~~The use of EBRM is aimed at specific rodent pest species and involves the timing of rodent control methods in the field based early in the crop cycle, as well as promoting farmers to work together as a community. EBRM comprises activities such as synchronizing planting of crops, development of trapping systems that intercept rodents as they move towards a deliberately planted high value food source,[9] destruction of rodent burrows, community trapping campaigns and scheduled trapping of rodents at key times of the year, particularly prior to the~~

5

onset of their main breeding season(s). [10-11] ~~Several~~Several Asian studies have

shown EBRM to be highly effective in diminishing rodent damage[9, 12-14] and have

~~proved to reduce~~reduced farmers' reliance on rodenticides. [9-10-11, 13, 15-14] ~~To date,~~

~~EBRM has traditionally focused on the pre-harvest stages of field cropping, while~~

~~strategies for the post-harvest stages of crop drying and storage are less~~

~~developed. [8, 16-17] Thus, post-harvest remains an area where novel EBRM options~~

~~need to be developed. Logically, there is no reason to restrict the management to~~

~~either the pre- or post-harvest stages of crops; it should be equally effective at~~

~~any time in identifying where placing control measures such as traps/baits would~~

~~be most effective. In the post-harvest period, rodents do not only cause losses to~~

~~harvested products, rodents contaminate a large percentage of the produce with~~

~~their droppings, urine, and saliva, which could possibly harbour pathogens. [16, 18-19]~~

~~Stored product damage by rodents often aggravates further deterioration of the~~

~~produce, as the food becomes more accessible to insects, moulds, and bacteria.~~

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. [11-15] 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, 11 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~~, and by that to~~

~~decrease the total amount of rodent damage in many countries.~~.

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 in spoiled sweet clover hay fed to cattle that subsequently suffered from internal bleeding. [20-21] The researchers went on to synthesise several analogues of dicoumarin leading to the compound known today as warfarin. According to Mills, (1955) the first controlled trials to kill rodents with warfarin took place in London in 1946-47.[22] Before long, researchers and rodent pest control companies realised that warfarin was far superior to the rat poisons previously used because rodents did not immediately feel ill after eating bait laced with warfarin. Thus rodents would continue to consume the bait until they ate a lethal dose. This is unlike the behaviour rodents show associated with more acute acting poisons; when a rodent feels immediately sick after eating a particular food laced with an acute poison, the rodent will often quickly feel ill, stop eating the poison before consuming a lethal dose and learn to avoid the poison, food bait and baiting location the rest of their lives. Furthermore, there is evidence that conspecifics of acutely poisoned rats can also learn to avoid such poisons. This learning behaviour of rodents based on an observational experience of another animal is called the "poisoned partner effect".[23] However, as many pest rodent species are omnivores and are inclined to eat broad variety of food types, including 'new' possible food items, a conflict of motivation occurs as they do not always know if a specific product is edible or not. This dilemma is known as the "omnivores paradox".[23] Some species of rodents can sometimes use social transmission of food preference to learn from each other as to which food sources cause illness.[24] However, for most omnivorous pest rodent species, cautious eating of small initial amounts of new foods is reinforced by the physiological inability to vomit that is common among all rodent species.[25]

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3   1   ~~Rodents have the capacity to link the taste and smell of food to how they feel,~~
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5   2   ~~even hours after consumption. Because rodents do not immediately feel ill after~~
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7   3   ~~eating bait laced with warfarin, warfarin and its modern-day anticoagulant~~
8
9   4   ~~analogues have become THE definitive tool for controlling rodents. Until the late~~
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11   5   ~~1980s, their efficacy and relative safety (if inadvertently ingested, domestic~~
12
13   6   ~~animals and humans can be treated with a vitamin K injection) certainly~~
14
15   7   ~~contributed to stifling other research avenues on rodent pest management such~~
16
17   8   ~~as developing more ecologically sound methods of rodent management. Besides,~~
18
19   9   ~~the use of rodenticides is an easy way of management. There is no need for daily~~
20
21   10   ~~checking. If farmers can afford to apply poisons in their fields then the only thing~~
22
23   11   ~~one needs to do is fill-up the poison-feeders once every 5-7 days. These factors~~
24
25   12   ~~explain why rodent control practices in agricultural environments are still mostly~~
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27   13   ~~based on the use of rodenticides.[8, 26-28] However, incorrect application of such~~
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29   14   ~~chemicals fast tracks the development of rodenticide resistance (reported from~~
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31   15   ~~1966 onwards for several rodent species) and increases the risk of both primary~~
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33   16   ~~and secondary poisoning of predators.[29] Because rodenticide use is a common~~
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35   17   ~~practice for rodent control, the need for EBRM increases even more.~~ (warfarin) in
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37   18   spoiled sweet clover hay fed to cattle that subsequently suffered from internal
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39   19   bleeding.[16-17] Because rodents do not immediately feel ill after eating bait laced
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41   20   with warfarin, warfarin and its modern-day anticoagulant analogues have become
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43   21   THE definitive tool for controlling rodents. Until the late 1980s, their efficacy and
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45   22   relative safety certainly contributed to stifling other research avenues on rodent
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47   23   pest management such as developing more ecologically sound methods of rodent
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49   24   management.[16] Rodent control practices in agricultural environments are still
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51   25   mostly based on the use of rodenticides.[8, 18-20] However, incorrect application of
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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.[11] Nevertheless, socio-cultural challenges of implementing EBRM do occur. For example, despite early-stage trapping being proven to be more effective than traditional reactive rodent killing, it is a general belief of farmers in developing countries that rodents appear suddenly in high numbers and that is when farmers feel the need to implement control. Such farmer practices appear to be driven by the belief that the more rodents they kill, the less damage will be done to their produce.[30-31] However, in other instances, some farmers report that rodents are the pest that they have the least control over and, therefore, the farmers simply accept that a loss of 5-15% is the norm.[32] Hence it is important to train farmers to increase their knowledge and change their beliefs in order to adjust the timing of their trapping activities or simply to encourage them to engage in management as a community. The EBRM spatio-temporal aspect is already[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

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1 rodent species (rodent species that are continuously present in the

2 neighbourhood of humans and cause losses to stored products and increased

3 risks of disease transmission) may be less than those of field rodent species, but

4 the spatio-temporal aspect of EBRM is still important. For example, if rodent

5 numbers are managed before agricultural produce is put into a storage facility, the

6 population growth of rodent pests and negative consequences to stored grain can

7 be significantly curtailed. Especially in the post-harvest situation, rodent

8 management should focus more on the behaviour of the pest rodent species than

9 on the current reactive methods. ~~With insight in population dynamics, predictive~~

10 ~~models could be established on which specific management methods can be~~

11 ~~developed.[33]~~ Again, more knowledge on pest species behaviour is needed for

12 ~~good implementation and results of management methods.~~ A behaviour all

13 animals have in common is the search for provisions. So what happens when one

14 focusses on species-specific foraging behaviour to gain more knowledge to

15 enable managing those pest-species?

16

2. SEARCH FOR PROVISIONS

18 The optimisation of foraging behaviour of animals addressing what food type

19 should be included in the diet was first published by Pianka and MacArthur ~~1966~~

20 ~~34~~[22] and Emlen.[~~35~~23] Charnov developed in 1976 the first optimal patch use model,

21 which is known as the Marginal Value Theorem (MVT).[~~36~~24] This theorem

22 hypothesizes that animals foraging assume that nutrition products occur in

23 clusters, and that ~~its~~their food consumption decreases linearly (but not constant)

24 with the time spent on that exact location. When making foraging decisions,

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1 animals balance the benefit of energy rewards and the price of predation.[37][25] The

2 MVT predicts that animals foraging in a patch will decide whether to depart is not

3 based on depletion of a food patch, but rather on the assessment of ~~the yield~~

4 ~~rate~~costs of ~~that~~foraging and the yield rate of the current patch versus the yield

5 rate of another 'new' food patch.[36, 38][24, 26] By creating food patches and assessing

6 the amount of food left after foraging, the giving-up density (GUD)[36] of a food

7 source becomes a measurable unit.[37, 39-40][25, 27-28] The GUD reflects the perceived

8 costs of foraging on that location. The more food left in a patch after the departure

9 of an animal, the higher the GUD, indicating high costs. ~~This GUD method~~

10 ~~provides insight in more than just the amount of resources harvested.[37] For~~

11 ~~example,~~[25] GUDs provide insights into the feeding behaviour and habitat

12 preferences of animals.[37, 41][25, 29] ~~Furthermore, GUDs also reveal the balance~~

13 ~~between food and safety; the metabolic costs of a foraging animal, its perceived~~

14 ~~predation risk during foraging, and the missed opportunity costs (MOC) of the~~

15 ~~forager by not engaging in activities other than foraging.[37, 42] With foraging yield~~

16 ~~being a direct function to food density, GUDs can be used as index of the~~

17 ~~forager's quitting harvest rate.[43-44]~~

18 Furthermore, GUDs also reveal the balance between food and safety; the

19 metabolic costs of a foraging animal, its perceived predation risk during foraging,

20 and the missed opportunity costs (MOC) of the forager by not engaging in

21 activities other than foraging.[25, 30] With feeding rate being a direct function to food

22 density, GUDs can be used as an index of the forager's quitting harvest rate.[31-32]

23

24 **2.1 Perceived predation risks**

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1. Because rodents can serve as prey for many different species of reptiles, birds

2. and mammals, they avoid places where the relative risk of predation is high. Both

3. indirect cues (e.g. vegetation cover, weather conditions, light intensity) as well as

4. direct cues (e.g. sound, odours, urine, or other excrements from potential

5. predators) enable rodents to assess predation risk during foraging behaviour.[45 33]

6. A study on the effect of owl predation on rodents' search for provisions in America

7. showed that adjustments in foraging behaviour as a response to perceived

8. predation risk are predominantly based on an awareness of the presence of a

9. predator, rather than on the actual capture or killing of prey by the predator.[37, 46]

10. This leads to more cautious behaviour of the forager than when no predator cues

11. are present.[25{Verdolin, 2006 #162, 34] Brown[3725] postulates that prey animals 'manage

12. risk' according to H = C + P + MOC, where H is harvest rate, C the metabolic

13. costs, and P stands for the costs of risk of predation. Research on foraging and

14. predation risk trade-off has been used in many different animal contexts, from

15. aquatic to terrestrial systems.[4735] A review in 2013 on GUD methodologies

16. discussed its use, practical benefits and drawbacks and gave insight into the

17. many species that have been studied (i.e. mule deer, *(Odocoileus hemionus)*, red

18. fox, *(Vulpes vulpes)*, voles, *(Microtus* spp. and *Myodes* spp., gerbils, *(Gerbillus*

19. *allenbyi)*, gold fish, *(Carassius auratus)*, squirrels, *(Tamiasciurus hudsonicus,*

20. *Callospermophilus lateralis,* and *Sciurus niger)*, mice, *(Rhabdomys pumilio,*

21. *Baeolophus bicolor, Acomys russatus, Acomys cahirinus* and *Peromyscus*

22. *maniculatus)*, possums, *(Trichosurus vulpecula)*, rats, *(Rattus fuscipes)*,

23. chipmunks).[48] *(Tamias minimus))*.[36] For all foraging animal species, the

24. perception of safety of feeding activities includes the encounter rate with

25. predators, the lethality of the predator, and the chance of surviving predation.[42, 49]

[54][30, 37-39] Prey animals continuously have to balance between demand for food and safety, e.g. reduced predation risk.[52][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[53][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.[4, 54] 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.*,[53][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.[55],[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. Besides, rodents have even more reasons to move within their habitat; for example reproduction is also an effector for movement. A male rodent will be more eager to leave his 'safe' location when he detects a female in heat, which will also have impact on 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).[42] The LOF reflects levels of fear of predation perceived by a prey species on different locations within

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its home range.[56] An example of the spatial dynamics of a LOF is the scatter

hoarding behaviour of grey squirrels through their trade-off of safer cache

locations (less pilferage) against an increase in predation risks. This way the

predators of the squirrels indirectly lead to the dispersal and establishment of

seedlings.[57] The LOF is species-specific; our assumption is that a spatial LOF will

look different for the grey squirrel than for the Norway rat 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, which leads to each

species having different predation costs of foraging (i.e. fear). As different rodent

species have different habitats and food-patch locations, the 3-D aspect of the

habitat use should be taken into account when setting up a measurement strategy

for perceived predation risk (e.g. GUDs). Makin *et al.*[44], for example, present the

LOF concept for studying the behaviour of vervet monkeys. By using GUDs they

show that the predation risk of these foraging animals results in a 3-dimensional

LOF as a result of fear of predation risk from both terrestrial as well as aerial

predators.[44] Furthermore, it is known that rodents alter their feeding patterns in

time in order to avoid predation. When combining the perceived risk of predation

with rodent behavioural responses, spatial use patterns of individuals could be

explained.[56] In applying these concepts to pest rodents, some rodent species,

e.g. Norway rats, 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.[58-59]

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

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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

15

1 Philippines.[6047] They concluded that bait or trap placement towards the centre of

2 rice crops that are typically <0.1 ha, would be more likely to be visited by rats.

3 Another study in wheat crops in Australia used GUDs to assess whether house

4 mice modified their habitat selection based on perceived predation risk.[29] Both

5 studies highlighted that a better understanding of factors influencing habitat use of

6 rodent pests could aid decisions on their management. What is lacking is

7 objective evidence on whether pest control strategies based on the habitat use of

8 pest rodents are more effective and have a more long-term effect than reactive

9 rodent management. We hypothesizesuggest that a better understanding of

10 rodent behavioural ecology, especially the concept of the LOF, will result in more

11 effective strategies for management of rodent pests. To be able to use the LOF in

12 management, it is essential to identify the possible advantages and

13 disadvantages, and current knowledge gaps of the LOF methodology, which can

14 point the way for further research.

15

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

17 **management tool**

18 A classic paper by Rosenzweig[6148] provides prescient advice for pest-managers

19 to take habitat selection into account in order to improve the management results

20 *"Pest populations may be controlled most cheaply by concentrating on their cradle*

21 *habitats (although natural selection might interfere)"[61])"[48]*, which is also stated

22 years later by Morris.[6249] As discussed earlier, not only habitat use plays a role

23 when developing successful management methods, but also foraging behaviours

24 should be taken into account as they provide reliable indicators for future

16

situations (more reliable than use of 'old' cues indicating the past).[6350] 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.[41, 6429, 51]

Although GUDs are tightly linked to habitat type, local population density may

yield very different outcomes. Competing 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.[65]

For example, two competing prey species using the same food patches can lead

to the same effect as avoidance of predation risk; the harvest yield[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.

Deteriorating The decrease of harvest yields will increase the value of energy

which leadslead to put more effort in foraging in a food patch which by GUDs

would be indicated as 'safe'.[6552] 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.[4129] These facts indicate the need to

evaluate inter-specific competition whilst measuring for predation risk behaviour of

foraging animals when using GUDs.[44, 65] As is assumed that bait uptake is related

to perceived risk, it means that a[32, 52] A low GUD indicates a 'safe place', which

might result in overconsumption there, whereas uptake of bait in riskier places

17

1
(high GUD) will be less. However, these dose rates might need to be adjusted to

2
deal with the consumption rate in response to this LOF induced effect. This is only

3
valid when a) there is no effect of density on GUDs; b) under-consumption does

4
not deliver the required dose or c) over-consumption matters. Simple measures

5
such as GUDs are generally cheap to conduct; however, there are several

6
important challenges in using GUDs that should be taken into account when

7
conducting and analysing measurements. Bedoya-Perez *et al.*[4836] indicated seven

8
important aspects that need careful consideration when using and interpreting

9
GUDs: (1) the relation between costs and benefits of the forager is not linear, but

10
not constant (e.g. curvilinear), (2) the forager's physical condition, (3) more than

11
one forager can visit a food patch simultaneously and sequentially, (4)

12
composition of the food-patch (nutritional value of the food and properties of the

13
substrate), (5) food patch predictability, (6) the forager's behaviours to maximize

14
fitness and overcome costs of searching for provisions, and (7) non-target species

15
foraging from food patches.[4836] Based on these shortcomings, it can be stated

16
that the use of GUDs to reflect foraging behaviour strategies of predator

17
avoidance[5240] cannot be assumed completely sufficient. However, it is

18
indisputably clear the GUDs are an effective tool to map a population's LOF,

19
which could be beneficial for pest-management. by providing objective

20
information on which to base decision making, collecting clear evidence of where

21
rodents are more or less likely to forage and how to manipulate habitats to

22
increase fear levels.

23

24
Another component of complexity is that some parasite species are able to

25
change the LOF of their hosts for the benefit of completing their life cycle. For

18

1   ~~example, the obligate parasite *Toxoplasma gondii* influences the LOF of rats by~~

2   ~~manipulating rodent (secondary host) behaviour in such a manner that the chance~~

3   ~~of being preyed upon by cats (final host) increases to ensure completion of its~~

4   ~~lifecycle, i.e. they become less fearful for cats (not only for the odour cats, but~~

5   ~~also during visual encounters with cats), with the parasite modifying the 'fight or~~

6   ~~flight' behaviour.~~ [66-67] ~~This type of parasite-induced host manipulation to enhance~~

7   ~~transmission to the final host is a clear example of the potential usage possibilities~~

8   ~~the LOF entails.~~

9   ~~Until now, current~~Current rodent management in agricultural and peri-urban

10 habitats have made little use of the LOF as an opportunity to strengthen pest

11 management. For example, intensity of rodenticide use and trapping could

12 decrease significantly if an understanding of the LOF is applied in the spatial

13 placement of such control interventions in agricultural landscapes. [~~60~~47] This is

14 particularly the case in developing countries where there have been few reports of

15 studies on the spatial and foraging behaviour of major rodent pest species.

16 ~~An essential part of rodent control is the placement of traps and baits.~~ Current

17 rodent trapping sometimes includes parts of the LOF implicitly, for example the

18 placement of traps along walls as it is known that most commensal rodents prefer

19 to move alongside walls. Trapping studies on micro-habitat use have tried to

20 reflect the concept of trap success depending on perceived predation risk.

21 However, still the most effective placement of rodent traps inside and around

22 buildings or within agricultural fields is generally based more on tacit knowledge of

23 the pest controller rather than rigorous data on the behaviour of the targeted pest

24 species in a landscape. ~~Van der Merwe and Brown~~ [~~68~~]Van der Merwe and

25 Brown[53] visualised the LOF of the cape ground squirrel via a physical map that

19

1 showed the predation costs of foraging (Figure 1a). A map of the LOF can show

2 valleys representing relative safety, and peaks which indicate perceived danger

3 (Figure 1b).[5644] In both graphics the LOF was used as a model to visualise how

4 fear could alter the area used by prey as it tries to reduce the risk of predation,

5 specifically during foraging.[53, 56, 6941, 44, 54] Within the LOF, animals will spend the

6 most time in the valleys, e.g. where the perceived predation risk is the lowest.

7 This information will enable rodent management to place traps on those specific

8 perceived low fear locations, which we hypothesizesuggest will increase trapping

9 rates and thus pest management success.

10 **{[Figure 1 could be placed around here}]**

11
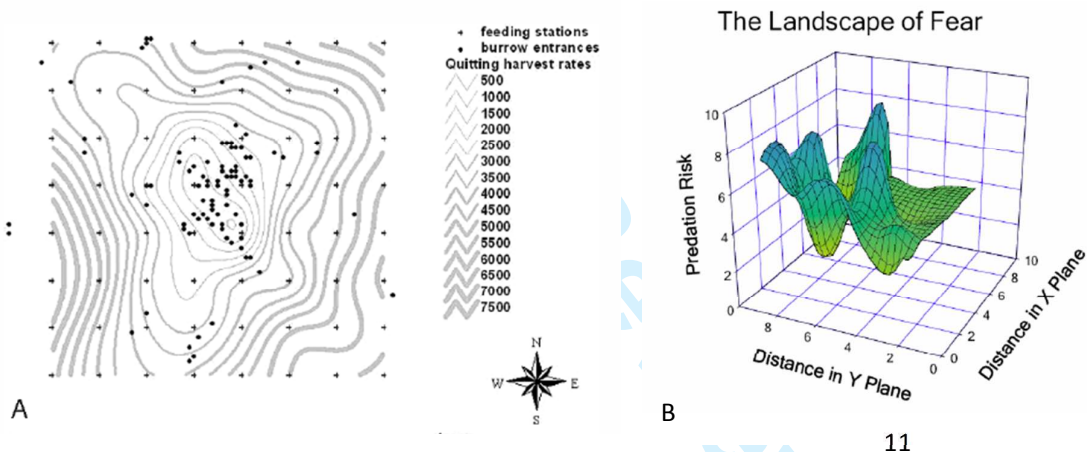
12 Figure 1. Two different ways of visualisation of the landscape of fear **A)** 2D map of the cape

13 ground squirrel, the thicker the grey line, the more 'safe' the squirrel feels to forage (adapted from

14 Merwe & Brown, 2008) **B)** 3D depiction of the landscape of fear, with highest giving up densities at

15 the peaks (retrieved from Laundré et al 2010).

16

17 Rodents can alter their risk management in twoseveral ways; (I) by time

18 allocation, e.g. shorten the exposure time and forage as fast and shortly as

19 possible to reduce predatorily encounters, and (II) by vigilance, e.g. reduce the

20

1   lethality of encounters with a predator, (III) by safety in numbers by synchronised

2   activity, and (IV) by night vs. day activity to avoid encounters with predators.

3   Again, trapping efficiency could be substantially improved if we had mapped the

4   LOF of the specific rodent pest species and then placed the traps accordingly (so

5   where GUDs are lowest[60] i.e.[47] i.e. peaks of the LOF). One option would be to

6   conduct a systematic analysis of the behaviour of pest species where their

7   ethology may help clarify potential actors in response to GUDs for LOF and

8   management actions for those species. Because the LOF differs peramong

9   species, it also differs between target and non-target rodents, which in termturn

10 could be used for minimising unwanted effects on non-targets. So again we point

11 out the need of mapping the LOF of the **specific** (pest) species one wants to

12 manage. In case of doubt, the LOF of the non-target species should also be

13 mapped to prevent trapping in overlapping perceived risk valleys. To date,

14 however, no study has systematically mapped the spatial behaviour of rodent pest

15 species where beneficial species would be at risk of non-target poisoning. In our

16 view, one should concentrate on the following four key points for the use of the

17 LOF as basis for rodent management (Figure 2):: (I) pest species with the lowest

18 GUD will be most easyeasiest to aim attarget, (II) species are most susceptible

19 during times of the year when their GUDs are lowest; during these intervals

20 management methods will be most effective, (III) species are most likely to be

21 trapped in (micro-) habitats where their GUDs are lowest; thus concentrate rodent

22 management (place the most traps/baits) on those areas where rodents perceive

23 the least levels of predation risk, and (IV) management strategies which increase

24 perceived risk of predation for the target pest species will lower pest damage, e.g.

25 biocontrol.. Measures to promote populations of appropriate predators should be

21

taken, such as placing out nest boxes for birds of prey (e.g. owls) and educating local communities about the benefit of local biological predators (e.g. foxes). Research into the use of "biocontrol" by domestic predators (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[70]. It was concluded that presence.[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.[70] [57] However, reliable scientific evidence that bio-control via predation minimizes rodent population size below damage threshold levels is not yet available.

{Figure 2 could be placed around here}

22
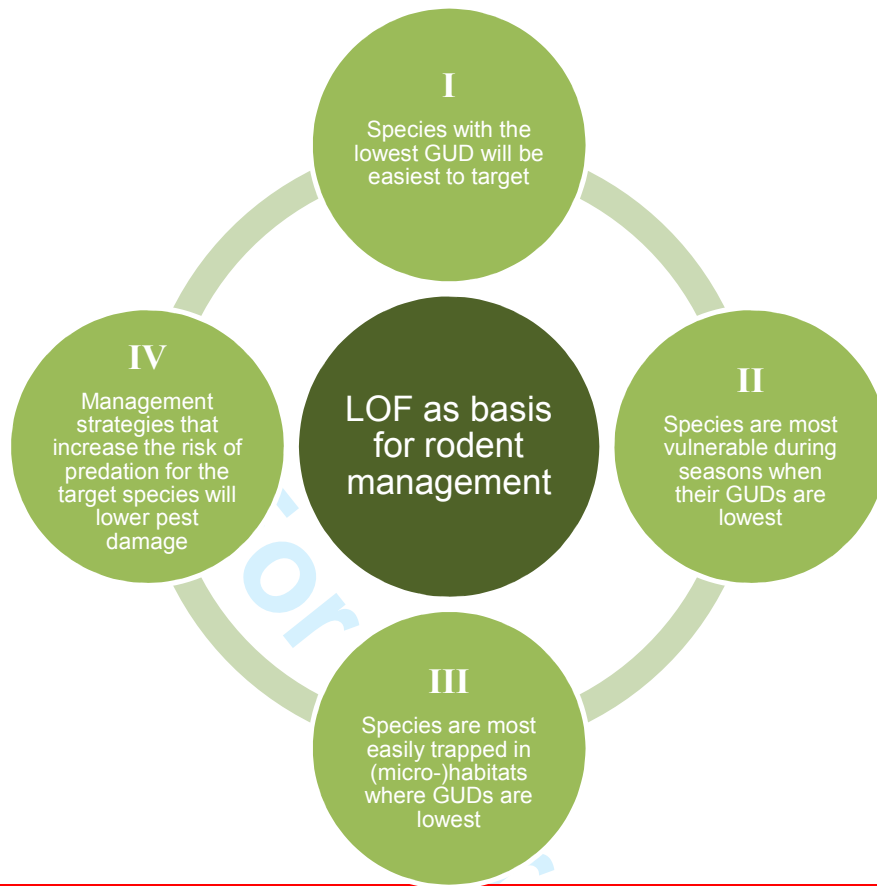
4   CONCLUSION

Connecting the LOF to the behaviour of rodent pest species is a novel approach with many opportunities to further enhance ecologically-based rodent pest management. Implementing the LOF into rodent management enablesmay 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-

23

1. management. A recent study of Mul et al.[33] developed a fully automated pest monitoring tool to implement IPM effectively. The study from Mul *et al.* also points out the need to align management methods with the pest-species biology and behaviour.[33][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.*[70]*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.

24

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2   development of this article.

3

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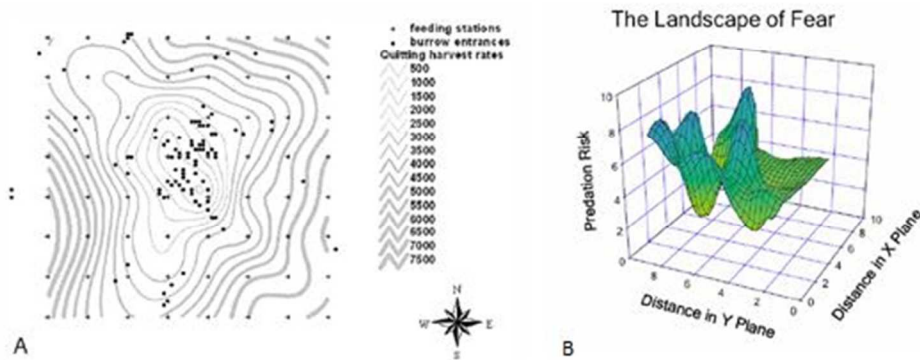33　Pest Management. in press.

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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).

149x65mm (96 x 96 DPI)