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Original Article

Efficiency of different spatial and temporal strategies for reducing vertebrate pest populations

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ABSTRACT

Understanding effectiveness of control strategies of pest species is fundamental for planning efficient and cost-effective management programs. In addition to culling rates, there are many potential factors that can determine efficiency of different management strategies, including demographic processes such as immigration rates, birth dynamics, and spatial ecology. We developed a stochastic, data-based simulation model of feral swine population dynamics which accounted for social dynamics in space. We tested the impacts of different spatio-temporal management strategies (i.e., culling rates, timing of culling during the year, spatial pattern of culling and strength of a barrier to immigration) on population response and efficiency. The spatial culling strategy dramatically impacted efficiency of control – using zonation required removal of fewer pigs (up to 46% less) to achieve similar reductions compared with other spatial strategies. Also, our spatially-explicit model predicted that lower culling intensities could be used to achieve population reductions when zonation was applied relative to predictions from harvesting theory based on simple logistic models. As culling intensity increased (≥50% of target population annually) and the target population reached low density (<5% of original density), effects of spatial strategy became less pronounced relative to immigration barrier effects. Lastly, for the same level of moderate culling effort, prioritization of culling during the low-birthing period generally resulted in faster population reduction to near zero abundance relative to prioritization during the high-birthing period, or spreading the work over a year period, but the significance of this effect depended on the spatial culling strategy and culling intensity. Our results imply that continually updating knowledge of current abundance during management may not only be important for determining culling quotas, but also for updating and optimizing management strategies. When the management goal is maximum population control, consideration of birth and spatial dynamics can increase return on management effort and bring to light management inefficiencies.

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1. Introduction

Determining effective strategies for reducing invasive or pest species is challenging due to complex population ecology in space and time. However, efficacy is not the only important management metric – identifying control strategies that maximize efficiency can be equally essential for satisfying control objectives because fiscal and personnel resources for many vertebrate pest control programs are limited. By interpreting the interplay of realistic ecological complexities, population models develop our mechanistic understanding of ecological conditions that affect the efficacy and efficiency of pest control, providing a science-based foundation for management planning. For example, population models have guided management by: identifying levels of culling pressure that limit population growth rate or abundance (Hone, 2012; Servanty et al., 2011; Gamelon et al., 2012), planning implementation of control techniques (Hone, 1990; Hone, 1992; Choquenot et al., 1993), evaluating combined control techniques (McCarthy et al., 2013; Yoak et al., 2016; Pepin et al., 2017), determining population densities that reduce damage (Hone, 2012; Krull et al., 2016), choosing spatial (McMahon et al., 2010) or temporal strategies (Grarock et al., 2014; Lieury et al., 2015), and planning strategies within the cost constraints of particular situations (Beeton et al., 2015; Anderson et al., 2016). In planning resource allocation for control of pests, primary questions include when, where and how much effort should be expended and how should it be distributed. There is a strong theoretical foundation for answers to some of

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these questions individually but a much weaker understanding of their combined effects, and effects of different spatial strategies are poorly understood in particular (Epanchin-Neill and Hastings, 2010). Thus, guiding principles for how to implement pest control in space and time remain elusive (Hone et al., 2015), which makes it difficult to plan pest control programs at the outset before much data are available.

Many wildlife species exhibit distinct seasonality in births (Zerbe et al., 2012), and conducting harvest at the wrong time can drive the population below a target abundance (Boyce et al., 1999; Kokko, 2001). The theory is based on the idea that after the birthing season there is an excess of individuals who are doomed to be lost naturally by density-dependent causes ('doomed excess', Errington, 1945), and thus hunting mortality compensates other types of mortality leading to a similar abundance the following year (Burnham and Anderson, 1984; Bartmann et al., 1992). Thus, conversely, if the goal is to substantially reduce the population efficiently, it is best to time culling when the population is at its lowest abundance, after the doomed excess have died (Grarock et al., 2014), when culling might have additive effects on total mortality. However, these effects have primarily been studied in populations with distinct birth pulses and it is less clear if similar guidelines would apply in populations with continuous or variable birth patterns.

Recent advances in conservation planning have highlighted the importance of spatial prioritization (prioritizing a particular spatial arrangement of control) in the success of conservation initiatives (Margules and Pressey, 2000; Moilanen et al., 2005). Conservation planning theory is partly based on metapopulation theory (Hanski and Ovaskainen, 2000), which shows that the fate of a metapopulation is determined by the connectivity of its component subpopulations. Although applicable, these concepts have been under-used for controling invasive species (Glen et al., 2013). In one example (Parkes et al., 2010) zoning was applied to eradicate wild pigs from an island, but the efficiency of zoning relative to other strategies was not investigated. Similarly, an analysis of spatial culling strategies suggested that prioritization of high-density areas is best (McMahon et al., 2010) but there appears to be no consensus on general guidelines for spatial prioritization (Epanchin-Neill and Hastings, 2010).

Wild pigs are an example of a vertebrate pest species with breeding seasonality that varies greatly depending on geographic location (Saunders, 1993; Gethoffer et al., 2007; Mayer and Brisbin, 2009; Macchi et al., 2010; Fonseca et al., 2011; Ježek et al., 2011; Orlowska et al., 2013; Lombardini et al., 2014), making them ideal for identifying general guidelines for when it is most efficient to cull (temporal prioritization). Wild pigs are also a social ungulate species exhibiting a wide range of family-group sizes, spatial dynamics (Podgórski et al., 2014a; Morelle et al., 2015; Kay et al., 2017) and territoriality (Sparklin et al., 2009), suggesting that their spatial population dynamics could provide a useful platform for developing guidelines for spatial prioritization of culling. Wild pigs are targeted for management in many countries due to their overabundance and damage to agriculture, humans and the environment (Campbell and Long, 2009; Barrios-Garcia and Ballari, 2012; Bevins et al., 2014). Several studies have documented different eradication strategies for wild pigs (Katahira et al., 1993; Lombardo and Faulkner, 2000; Cruz et al., 2005; McCann and Garcelon, 2008; Parkes et al., 2010), providing a strong foundation for planning efficient culling programs. However, these empirical studies were not able to evaluate whether alternative strategies would have been more efficient, or provide insight into planning maximum control in areas with strong immigration pressure (e.g., Delgado-Acevedo et al., 2013; Bodenchuk, 2014). Similarly, models of wild pig population control have been helpful at guiding the implementation of different lethal control tools (Hone, 1992; Choquenot et al., 1993; Choquenot et al., 1999), but general guidance on when, where and how much remains limited, especially in landscapes with immigration (Delgado-Acevedo et al., 2013).

To facilitate the planning and resource allocation for controlling a social, vertebrate pest such as wild pigs, we examined the efficiency of different realistic management strategies in space and time. To address a new level of complexity with this problem, we considered multiple aspects of management implementation in a full-factorial design, by varying culling intensity, timing, spatial prioritization, and immigration control. We examined these scenarios in landscapes with different patch sizes (differing by carrying capacity) and in populations with different birth patterns (pulse versus continuous) to investigate whether general guidelines emerged. In line with previous work (Grarock et al., 2014), we hypothesized that focusing culling during months when abundance was low (pre-births) would be more efficient than focusing culling during months when births were high (post-births) because resources would not be wasted on the doomed excess (Boyce et al., 1999). We sought to determine if this hypothesis held true for populations with more continuous birth seasonality that includes multiple peaks (Gethoffer et al., 2007; Mayer and Brisbin, 2009; Macchi et al., 2010; Orlowska et al., 2013), relative to ones with a more focused birth pulse (Fonseca et al., 2011; Lombardini et al., 2014), upon which the hypothesis has been formulated. We also investigated whether zoning would be more effective than spatially random strategies or strategies that target high-density patches, because zoning is applied in practice (Parkes et al., 2010) but its benefits relative to other spatial methods are poorly understood (Epanchin-Neill and Hastings, 2010). As many population control scenarios are not conducted in areas closed to re-invasion, we also compared effects of different culling patterns with and without immigration from surrounding populations.

2. Methods

To identify efficient management outcomes that consider the complex ecological processes of social, vertebrate-pest species, we developed an individual-based model (IBM) which explicitly accounted for individual-level variation in movement behavior, reproduction, social dynamics, and shifts in space. All analyses were conducted using Matlab R2016b (Version 9.1.0, The MathWorks, Inc., Natick, MA). Below we describe our approach using the updated Overview, Design concepts, and Details (ODD) protocol for individual-based models (Grimm et al., 2010).

2.1. Purpose

Our goals were to 1) understand how different spatio-temporal strategies of vertebrate-pest management determine the effectiveness and efficiency of population reduction given birth seasonality, social and spatial dynamics, and 2) identify efficient strategies for greatly reducing vertebrate pests in landscapes with immigration. For our case study, we were interested in reducing the population substantially, which we evaluated by how much the population was reduced within 5 years and how much effort/time was required to reduce the population by 90%. Specifically, we set out to answer:

- Is it efficient to time culling activities relative to birth seasonality, and if so, what timing is most efficient?
- Considering social dynamics and landscape patchiness, is there a spatial culling pattern which is most efficient, and if so, what is it?
- What combination of culling intensity and immigration barrier allows a particular population management goal to be reached efficiently?