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FROM PRACTICE

*Ov*CWD: An agent-based modeling framework for informing chronic wasting disease management in white-tailed deer populations

Aniruddha V. Belsare[1] | Chad M. Stewart[2]

[1] Boone & Crockett Quantitative Wildlife Center, Department of Fisheries & Wildlife, Michigan State University, East Lansing, Michigan

[2] Michigan Department of Natural Resources, Lansing, Michigan

Correspondence
Aniruddha Belsare, Boone & Crockett Quantitative Wildlife Center, Department of Fisheries & Wildlife, Michigan State University, East Lansing, MI 48824.
Email belsare1@msu.edu

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Abstract

1. Wildlife diseases are gathering attention worldwide due to their public health and economic or conservation impacts, and consequently, wildlife agencies are increasingly being tasked with disease surveillance and management responsibilities.
2. Wildlife disease surveillance and management is challenging primarily due to complex processes of host population dynamics, some of which are inherently stochastic in nature. Individual heterogeneity in pathogen transmission further complicates our understanding of wildlife disease systems.
3. Agent-based models can incorporate stochasticity as well as individual heterogeneities and facilitate a better understanding of epidemiological processes in wildlife disease systems. Such an understanding is critical for designing and implementing effective disease control strategies.
4. We have developed a customizable agent-based modeling framework (*Ov*CWD) that incorporates nonrandom and heterogeneous aspects of an emerging host–pathogen system (chronic wasting disease [CWD] in white-tailed deer). Models in this framework link white-tailed deer demography and behavior with CWD transmission dynamics. Insights gained from model explorations can help us better understand CWD spread in regional deer populations.
5. We illustrate *Ov*CWD application by deriving CWD outbreak probabilities for Montcalm County (Michigan, USA) deer population using alternate harvest strategies. The focus is on preemptive harvest strategies that can be implemented before CWD is detected in a population (pre-establishment phase).
6. *Ov*CWD provides a defensible decision-making context for designing locally relevant CWD control strategies. *Ov*CWD can be readily adapted for simulating CWD in other cervid species as well as for simulating other cervid disease systems.

KEYWORDS
agent-based models, behavior, chronic wasting disease, demography, social structure, transmission, white-tailed deer

1 | INTRODUCTION

There has been a growing recognition that infectious diseases of wildlife can pose significant risks to the health of humans, domestic species, and wildlife populations (Cunningham, Daszak, & Wood, 2017). Consequently, wildlife agencies around the world are increasingly involved in adopting and implementing strategies for management of wildlife diseases. A recent example is chronic wasting disease (CWD), an emerging prion disease that has been detected in free-ranging and captive cervids in 26 U.S. states and three Canadian provinces as well as in South Korea, Norway, Finland, and Sweden. Continued discoveries of new CWD foci in captive and wild populations highlight the need for reliable and sustainable CWD management strategies. However, considerable uncertainty remains about the mechanisms and factors driving the transmission of this disease. Furthermore, CWD control interventions for wild cervid populations are limited by logistical, financial, and sociopolitical considerations. So far, CWD management strategies have mostly focused on restricting products that could serve as a potential source of infectious prions (bait, urine, etc.) and reducing host densities through a combination of hunter harvest and targeted culling. The success of such CWD control strategies in mitigating the spread of CWD remains to be evaluated.

The spread and establishment of infectious wildlife diseases is influenced by complex host population dynamics (LaDeau, Glass, Hobbs, Latimer, & Ostfeld, 2011). Mathematical and simulation models can help improve our understanding of disease dynamics and outbreak probabilities in host populations. Moreover, model-based approaches are critical for evaluating and designing wildlife disease management strategies (Vicente et al., 2019). We have developed an agent-based modeling framework (*Ov*CWD) that facilitates the linking of host demography, host behavior, and CWD transmission, and provides a decision-making context for evaluating CWD management strategies. An important feature of *Ov*CWD is the ability to simulate age–sex-specific scenarios and interventions, as relevant individual host characteristics (age, sex, group membership) and behaviors (dispersal, grouping behavior) have been incorporated in the model programs.

This modeling framework was developed for, and in collaboration with, agency biologists and managers. Model programs have a user-friendly graphical user interface, and the interface sliders and choices allow users (even non-modelers) to update model assumptions and perform virtual experiments. Furthermore, the constituent models can be setup using Geographic Information Systems (GIS) coverage data (forest cover) for any region of interest. In fact, *Ov*CWD builds upon models that were developed for evaluating CWD surveillance in Missouri's white-tailed deer populations (Belsare et al., 2020). *Ov*CWD can be readily adapted for simulating CWD in other cervid species as well as for simulating other cervid disease systems.

Here, we describe the component models of *Ov*CWD and illustrate how this framework can be used to evaluate strategies designed to control CWD in the early (pre-establishment) stage of the outbreak.

2 | COMPONENT MODELS

*Ov*CWD comprises two agent-based models, *Ov*POP (***O** docoileus **v** irginianus* **POP**ulation simulation model) and *Ov*CWDdy (***O** docoileus **v** irginianus* **C**hronic **W**asting **D**isease dynamics model). Both the models are coded in the high-level language NetLogo (Wilensky, 2010). As the models described here have been adapted to simulate Michigan's white-tailed deer populations, we refer to them as MI*Ov*POP and MI*Ov*CWDdy, respectively (Belsare, 2019a, 2019b).

The population simulation model incorporates geographic data, demography, and dynamic social structure of white-tailed deer to generate realistic *in silico* deer populations, and MI*Ov*CWDdy uses the MI*Ov*POP-generated population snapshot to simulate CWD transmission across deer contact networks in the model deer population.

2.1 | Population dynamics

In both models, population dynamics is defined by two sets of user-specified age–sex-specific parameters, *hunting mortality rates* and *nonhunting mortality rates*. Hunting mortality rates are annual, whereas nonhunting mortality rates are monthly. Mortality is a stochastic event in both the models as individual deer are subject to mortality probabilities during each time step. In addition to hunting and nonhunting mortality, infected deer in MI*Ov*CWDdy model are subjected to disease-related mortality within a month after they start exhibiting overt clinical signs of CWD.

2.2 | CWD introduction and progression

CWD is introduced in the model deer population in the sixth month of the first year. The user specifies the number and characteristics (age–sex class and group association) of deer that are initially infected (slider "seed-infection" and chooser "CWD_introduced_by" on the model interface).

Efficient animal-to-animal (horizontal or direct) transmission of infectious prions facilitates CWD spread across contact networks in deer populations (Altizer et al., 2003; Cross et al., 2009; Tamgüney et al., 2009; Williams, 2005). Although CWD can be transmitted indirectly (via environmental contamination), direct (animal-to-animal) transmission appears to be the dominant mechanism of disease spread in the early stages of CWD outbreak (Almberg, Cross, Johnson, Heisey, & Richards, 2011; Schauber, Nielsen, Kjær, Anderson, & Storm, 2015). As these models were developed to specifically simulate the pre-establishment stage of CWD outbreaks, only direct deer-to-deer transmission is included in the model program.

The duration of CWD phases in individual deer is modeled stochastically based on published ranges documented for experimental infections. The pre-infectious phase (duration from exposure to first excretion of CWD prions) in the model deer ranges between 6 and

10 months (Plummer, Wright, Johnson, Pedersen, & Samuel, 2017) and the preclinical phase (from exposure to the onset of overt clinical signs) ranges between 21 and 25 months (Johnson et al., 2011).

2.3 | Behavior

Dispersal behavior is included in both the models as it is a critical function of white-tailed deer ecology, and it creates opportunities for transmission and the spread of pathogens (Cullingham et al., 2011). Every year of the model run, yearling buck and yearling female dispersal is scheduled before parturition in the fifth month. Additionally, yearling buck dispersal also occurs before rutting activity in the 11th month every year. Dispersal rates for yearling bucks and yearling females are extrapolated from published literature, and set using two model parameters: *yearling-male-dispersal-rate* and *yearling-female-dispersal-rate*. Dispersal distances for yearling bucks are modeled using percent forest cover, as suggested by Diefenbach, Long, Rosenberry, Wallingford, and Smith (2008). Dispersal distance for juvenile female is derived from a random distribution with a mean of 11 miles and a standard deviation of 4 miles (Lutz, Diefenbach, & Rosenberry, 2015). Dispersing individuals travel the calculated dispersal distance as an equivalent number of patches in a random direction. We assume that the number of individuals dispersing out of the model landscape is equal to the number of individuals dispersing into the model landscape. Therefore, at any point during dispersal, if a deer moves past the edge of the model landscape (world wraps horizontally as well as vertically), it reappears on the opposite edge as a different deer. If a dispersing deer reaches a non-deer occupancy patch, it is transferred to the nearest deer occupancy patch.

2.4 | Social interactions

Group dynamics and sociality are important in the context of simulating within- and between-group interactions in the model deer population.

Aside from rutting behavior and pursuit of adult female deer, adult male deer are solitary during breeding season, but otherwise form temporary bachelor groups of nonrelated individuals (Hirth, 1977). During model simulations, bachelor groups are formed during the first month every year and break down in the 10th month before the rutting season. Bachelor group leaders assess their group's membership every time step (except months 10, 11, and 12), and lose the leadership status if no other members exist.

Doe social groups update, and if necessary, regulate their group size after the fawning season (month = 5). If the group size is greater than 6, up to two female group members (adults or yearling) along with their fawns lose group affiliation and become solitary with changed contact structure. Designated leaders of doe social groups with four or less members increase their group size by seeking solitary females in a 1.5-mile radius (Moore neighborhood) and adding up to two females along with their newborn fawns to the group.

2.5 | Contact structure

A contact matrix informs infectious–susceptible deer contact probabilities in *Ov*CWDdy (Figure 1; see Supporting information, ODD for MI*Ov*CWD, table 4). This contact matrix is user customizable and facilitates the incorporation of updated information or alternate assumptions about deer contact structure. For instance, potential regulation changes that affect contact rates within and between groups, such as baiting and feeding bans, can be easily evaluated using this feature.

Seasonal fluctuations in the pattern and strength of social affiliations are considered while building the contact matrix for white-tailed deer. Specifically,

1. The strongest associations within a doe social group are between females and their young and between sibling juveniles (Hawkins & Klimstra, 1970). Social interactions such as allogrooming may play a role in CWD transmission as infectious deer shed prions in their saliva, urine, and feces (Haley, Mathiason, Zabel, Telling, & Hoover, 2009; Mathiason et al., 2006; Tamgüney et al., 2009).
2. Newborn fawns have a close association with their mother as nursing occurs two to six times a day during the first month (Jackson, White, & Knowlton, 1972). We estimate a minimum of 60 and a maximum of 90 contacts over a month between a doe and her fawn of age 1 month or less. As the probability of transmission given an infectious contact is set at .0128 (Kjær, 2010), more than 80 infectious contacts per month results into a CWD transmission probability of one. Full siblings bed separately during their first month but start appearing together after they are a month old (Schwede, Hendrichs, & Wemmer, 1994). We do not simulate contacts between siblings less than a month old.
3. Fawns interact with siblings, and social play is common (Jacobson, 1994). Fawns are weaned when they are 3-month old (DeYoung & Miller, 2011). Postweaning, male fawns associate less and more loosely with their mothers than female fawns (Schwede et al., 1994).
4. Doe social groups remain together year around except during the fawning season when parturient females isolate themselves (Hawkins & Klimstra, 1970; Nelson & Mech, 1981; Ozoga, Verme, & Bienz, 1982). Within-group contact probabilities are high during the gestation period and low during the fawning season.
5. Between-group contact rates for does are estimated from Kjær, Schauber, and Nielsen (2008).
6. Yearling and adult bucks tend to be segregated from doe social groups except during the rutting season when courting males pursue and form tending bonds with receptive females (Kie & Bowyer, 1999; Smith, 1991). Except for the rutting season, bucks and yearlings occur in loosely associated bachelor groups (Hirth, 1977).

2.6 | Mating

In MI*Ov*CWDdy, CWD transmission can occur during mating interactions. Given the short and synchronized estrous period of

PERIOD	Age in months	MOM	FAWN(m)	FAWN(f)	FULLSIB(m)	FULLSIB(f)	NONSIB(m)	NONSIB(f)	GROUP(f)	NONGROUP(f)	BUCKS
GESTATION											
male fawn	9-12	5-10	0	0	10-20	5-10	10-20	5-10	0-5	0	0
female fawn	9-12	10-20	0	0	5-10	10-20	5-10	10-20	5-10	0-5	0
male yearling	21-24	0	0	0	0	0	0	0	0	0	1-5
female yearling	21-24	10-20	5-10	10-20	0	10-20	0	0	5-20	0-5	0
Buck	> 32	0	0	0	0	0	0	0	0	0	5-15
Doe	> 32	0-10	5-10	10-20	0	0	0	0	5-10	0-5	0
FAWNING											
male yearling	13-14	0	0	0	10-20	5-10*	10-20	5-10*	0	5-10*	0
female yearling	13-14 no fawns	0	0	0	5-10	10-20*	5-10	10-20*	5-10*	0	0
female yearling	13-14	0	60-90	60-90	0	0	0	0	0	0	0
Buck	> 26	0	0	0	0	0	0	0	0	0	5-15
Doe	> 26	0	60-90	60-90	0	0	0	0	0	0	0
Doe	25-26 no fawns	0	0	0	0	5-10*	0	0	5-10*	0	0
WEANING											
male fawn	3	60-90	0	0	60-90	60-90	0	0	5-10	0	0
female fawn	3	60-90	0	0	60-90	60-90	0	0	5-10	0	0
male yearling	15	0	0	0	0	0	0	0	0	0	1-5
female yearling	15	10-20	60-90	60-90	0	10-20	0	0	5-10	0-5	0
Buck	> 26	0	0	0	0	0	0	0	0	0	5-15
Doe	> 26	0-10	60-90	60-90	0	0	0	0	5-10	0-5	0
PRERUT											
male fawn	4-6	10-20	0	0	30-50	30-50	10-20	5-10	5-10	0	0
female fawn	4-6	20-30	0	0	30-50	30-50	5-10	20-30	10-20	0	0
male yearling	16-18	0	0	0	0	0	0	0	0	0	1-5
female yearling	16-18	10-20	10-20	20-30	0	10-20	0	0	5-10	0-5	0
Buck	> 28	0	0	0	0	0	0	0	0	0	5-15
Doe		0-10	10-20	20-30	0	0	0	0	5-10	0-5	0
RUT											
male fawn	7,8	0-5	0	0	10-20	0-5	10-20	0-5	0-5	0	0
female fawn	7,8	5-10	0	0	0-5	10-20	0-5	10-20	0-5	0	0-10
female yearling	19,20	0-5	0-5	5-10	0	0-5	0	0	5-10	5-8	0-15
Buck	> 15	0	0	0	0	0	0	0	0	0	0
Doe	> 26	0-5	0-5	5-10	0	0	0	0	0-5	5-8	5-30

FIGURE 1 Contact matrix (contactstructure.csv) provides the range of the number of contacts per month an infectious individual (first column) makes with susceptible deer (columns 3–12). The number of contacts are derived from literature or expert opinions. An asterisk (*) indicates susceptible females without fawns during the fawning season

1–2 days when females are receptive (Hirth, 1977), and the nature of prebreeding interactions such as the formation of tending bonds by courting males, breeding females in the model population interact with one to three breeding males during the rutting season. Similarly, mature bucks (>2.5 years old) interact with one to six females, whereas young bucks (1.5 to 2.5 years old) interact with one to three females during the rutting season. Presence of CWD prions has been documented in semen and sexual tissues of infected white-tailed deer bucks (Kramm et al., 2019). We therefore assume that the CWD transmission probability is higher for infectious male-susceptible female mating interactions compared to infectious female-susceptible male mating interactions.

3 | MODEL OUTPUT

MIO*v*POP simulates deer population dynamics for 15 years and exports a postharvest population snapshot of the model deer population (.csv file). Values of all deer and patch variables, both built-in and user-defined, are written in the file. This file can be read back into NetLogo.

MIO*v*CWDdy simulates population and CWD dynamics for 10 years and documents the following for each year in an output file (.csv): preharvest abundance, age–sex-specific harvest rates, number of CWD+ deer in the population before harvest, number of patches that have CWD+ deer, number of CWD+ deer in the harvest, number of harvested deer that were tested for CWD, and number of CWD+ deer in the test samples. These outputs can be used to derive CWD prevalence, rate of CWD spread (change in prevalence as well as geographic spread), and CWD outbreak probability in the model deer population.

4 | IMPLEMENTATION

MIO*v*POP and MIO*v*CWDdy were both developed in NetLogo 6.0, a software platform for implementing agent-based models (Wilensky, 2010). Complete model code and documentation for the two component models are available via website repository "Open ABM CoMSES Computational Model Library" (Belsare, 2019a, 2019b). The ODD (Overview, Design concepts, and Details) protocol for both the models is provided as Supporting Information.

For basic validation, we initialized MIO*v*POP to simulate the Montcalm County (Michigan, USA) deer population using population parameters derived from harvest data (unpublished data, Michigan Department of Natural Resources), peer-reviewed literature, or expert opinions (see Supporting information, ODD protocol MIO*v*POP). Each model run was for 25 years. We analyzed postharvest population

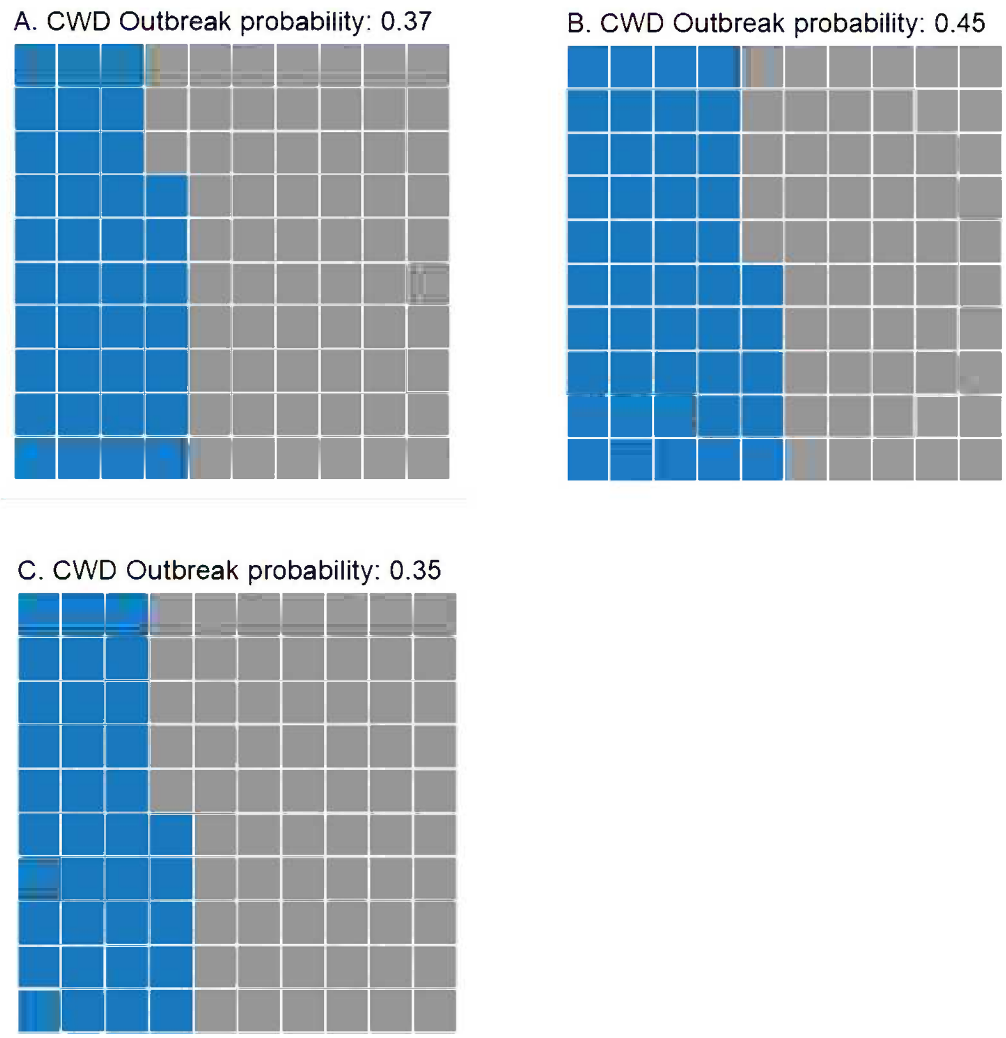

FIGURE 2 Waffle plots illustrating model-derived CWD outbreak probabilities for three harvest scenarios (a) current harvest, (b) Antler Point Restriction (APR), and (c) increased yearling male harvest. Each square represents one model iteration; blue color indicates CWD outbreaks that persisted throughout the 10 years of model simulation

snapshots obtained from 10 model iterations to assess the congruence of model-generated population parameters with field estimates (see Figures S1–S3 and Table S1).

Sensitivity analysis was performed for MI*Ov*CWD using an index that incorporates output variance in the local sensitivity analysis (Bar Massada & Carmel, 2008). In brief, deer-to-deer transmission events were particularly sensitive to the CWD transmission probability (Table S2). Details are provided in Supporting Information.

MI*Ov*CWDdy was initialized with a MI*Ov*POP-generated snapshot of the Montcalm County deer population. CWD was introduced in the fully susceptible model deer population during the first year of the model run via one dispersing male yearling. MI*Ov*CWDdy was simulated for a period of 10 years to assess the impact of current harvest strategy on deer demographics, and thereby on the population resiliency to the spread or establishment of CWD. We recommend using the metric "CWD outbreak probability" to quantify population resiliency to CWD spread. CWD outbreak probability is derived using an iterative approach as the proportion of iterations with persistent CWD outbreak throughout the model run. CWD outbreak probability for Montcalm County deer population derived using this model was 0.37, assuming an early stage of CWD invasion and no changes in the current harvest strategy (Figure 2A).

5 | STUDY EXAMPLE

We now illustrate how model-based explorations can be used to compare and contrast alternative harvest strategies, and thereby inform the design of locally relevant CWD control policies. The invasion process of emerging wildlife diseases such as CWD can be divided into four distinct stages: pre-arrival, invasion front, epidemic, and established (Langwig et al., 2015). CWD is difficult to detect in the early stages of the outbreak with active surveillance as it occurs at a low prevalence with focal areas of infection near the point of introduction (Samuel et al., 2003; Walsh, 2012). By the time active surveillance detects CWD, it is already established and nearly impossible to eliminate

(Miller & Fischer, 2016). The best chance of controlling CWD outbreak is therefore in the early phase of the outbreak, the predetection phase.

*Ov*CWDdy facilitates the evaluation of alternate harvest strategies on deer demographics, and how the changed structure of the deer population affects the spread and persistence of CWD. The objective is to identify locally implementable harvest strategy achieving the lowest CWD outbreak probability.

Here, we evaluate two harvest strategies for Montcalm County deer population using MI*Ov*CWDdy: (a) reduced yearling buck harvest rate (32%) under an antler points restriction (APR) regulation and (b) increased yearling buck harvest rate (55%). Current yearling male harvest rate for Montcalm County is 47%. The two scenarios represent examples of decisions state management agencies face when attempting to develop strategies to manage deer herds in a potential CWD area.

APR regulation is designed to increase age structure of males in the population. Under an APR regulation, hunters are required to harvest only antlered deer with a specified minimum number of antler points. The number of points is determined using harvest data and is intended to protect at least 50% of yearling bucks on the landscape. With generally low nonhunting mortality for these yearling deer protected through their first hunting season, APRs result in an increase in the age class of antlered deer on the landscape.

Using the same steps (described under Implementation), we determined CWD outbreak probabilities for the two harvest strategies. Population resiliency to CWD spread decreased under the APR scenario (CWD outbreak probability increased to 0.45; Figure 2B), whereas under the increased yearling male harvest scenario population resiliency to CWD spread increased (CWD outbreak probability decreased to 0.35; Figure 2C).

Harvest emphasis on young males does appear to be a viable strategy for CWD control. However, this approach is often in direct conflict with desires of many hunters, who prefer to pursue older-aged males that typically exhibit larger antlers. *Ov*CWDdy provides wildlife managers an opportunity to evaluate more nuanced harvest scenarios (reduced yearling buck harvest rate + increased antlerless harvest) so as to identify locally acceptable strategies that build resiliency to CWD spread and establishment in the deer herd.

6 | CONCLUSION

Model-based evaluations can support the design of defensible, locally relevant wildlife disease control strategies. Alternate harvest strategies can be compared and contrasted using model-derived metrics such as CWD prevalence, rate of spread, and CWD outbreak probability. Such predictive comparison can benefit wildlife managers, who can now bring forward defensible recommendations for deer and disease management that previously have not existed.

Effective intervention requires merging research and management actions in an adaptive management framework. *Ov*CWD framework represents a unique adaptive management tool as the constituent models are customizable and allow the users to update model assumptions based on their current best knowledge of the system. The model allows agencies to engage in discussions with stakeholders by showing them likely benefits and consequences of deer management regulations and how it can impact CWD spread. This allows opportunities for responsible stakeholder involvement while designing CWD control strategies. With aggressive management responses historically proving unfavorable among the hunting public and often discontinued based on social and/or political pressures, there is a need for agencies to develop socially acceptable yet biologically responsible recommendations when responding to CWD outbreaks.

AUTHOR CONTRIBUTIONS

AB developed the models. AB and CS conceived the model applications. CS collected the data. AB and CS led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

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PEER REVIEW

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DATA AVAILABILITY STATEMENTS

Model codes for *Ov*POP and *Ov*CWDdy, GIS data for the Michigan version, and detailed ODD (Overview, Design concepts, and Details) protocols are available for download via the CoMSES Net Computational Model Library: https://doi.org/10.25937/6qeq-1c13 and https://doi.org/10.25937/kv07-3e08 (Belsare, 2019a; 2019b).

ORCID

Aniruddha V. Belsare https://orcid.org/0000-0002-4651-0116

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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