

A PDE MODEL OF INTRAGUILD PREDATION WITH CROSS-DIFFUSION

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ABSTRACT. This note concerns a quasilinear parabolic system modeling an intraguild predation community in a focal habitat in \mathbb{R}^n , $n \geq 2$. In this system the intraguild prey employs a fitness-based dispersal strategy whereby the intraguild prey moves away from a locale when predation risk is high enough to render the locale undesirable for resource acquisition. The system modifies the model considered in Ryan and Cantrell (2015) by adding an element of mutual interference among predators to the functional response terms in the model, thereby switching from Holling II forms to Beddington-DeAngelis forms. We show that the resulting system can be realized as a semi-dynamical system with a global attractor for any $n \geq 2$. In contrast, the original model was restricted to two dimensional spatial habitats. The permanence of the intraguild prey then follows as in Ryan and Cantrell by means of the Acyclicity Theorem of Persistence Theory.

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1. **A Quasilinear System of PDE.** Let $n \geq 2$ and Ω be a bounded smooth domain in \mathbb{R}^n . In this paper we consider initial-boundary value problem for the following quasilinear system of partial differential equations modeling intraguild predation.

$$\begin{cases} u_t - d_1 \Delta u = f(x, u, v, w)u & \text{in } \Omega \times (0, T), \\ v_t - \Delta[M(u, v, w; \lambda)v] = g(u, v, w)v & \text{in } \Omega \times (0, T), \\ w_t - d_3 \Delta w = h(u, v, w)w & \text{in } \Omega \times (0, T), \\ \partial_\nu u = \partial_\nu v = \partial_\nu w = 0 & \text{on } \partial\Omega \times (0, T), \\ (u(x, 0), v(x, 0), w(x, 0)) = (u_0(x), v_0(x), w_0(x)) & \text{in } \Omega, \end{cases} \quad (1)$$

where $T > 0$ is the maximal time of existence and ν denotes the outer normal vector on $\partial\Omega$. Here $u(x, t)$ is the density of the resource species, which is consumed by both the intraguild prey with density $v(x, t)$ and intraguild predator with density $w(x, t)$, while the intraguild prey is also consumed by the intraguild predator, as indicated by the definitions of f, g and h below:

$$f(x, u, v, w) = r(x) - \omega_1 u - \frac{a_1 v}{1 + h_1 a_1 u + \alpha_1 v} - \frac{a_2 w}{1 + h_2 a_2 u + h_3 a_3 v + \alpha_2 w}, \quad (2)$$

$$g(u, v, w) = \frac{e_1 a_1 u}{1 + h_1 a_1 u + \alpha_1 v} - \frac{a_3 w}{1 + h_2 a_2 u + h_3 a_3 v + \alpha_2 w} - \mu_1 - \omega_2 v, \quad (3)$$

$$h(u, v, w) = \frac{e_2 a_2 u + e_3 a_3 v}{1 + h_2 a_2 u + h_3 a_3 v + \alpha_2 w} - \mu_2 - \omega_3 w, \quad (4)$$

where all parameters $a_j, \alpha_j, h_j, e_j, \mu_j, \omega_j$ are positive constants. The resource species and the intraguild predator are assumed to disperse unconditionally with rates d_1 and d_3 respectively, while the intraguild prey adopts a conditional dispersal strategy that balances resource availability, predation avoidance and possibly (intraspecific) population pressure. The specific form of $M(u, v, w; \lambda)$ will be presented in the main results section.

2. **Background.** Intraguild predation is an important community module in ecology. It refers to a situation in which a predator and a prey also compete for a shared resource (i.e., they are members of an ecological guild). As discussed in [6], intraguild predation is widely observed in nature across a broad range of taxa. Indeed, in the database of 113 food webs that were examined in [6], intraguild predation occurs in high frequency.

Despite the ubiquity of intraguild predation in nature, the early efforts of Holt and Polis [11] to set up an ODE system based modeling framework for intraguild predation found that such a model was particularly prone to species exclusions. Holt and Polis suggested a number of possible mitigating factors that might enhance the chance of species coexistence. One of these was to allow for a heterogeneous environment. Somewhat contemporaneously, numerous empirical studies reinforced this suggestion through the observation of nonrandom foraging behaviors and habitat selection on the part of the intraguild prey species to reduce predation risk ([8, 15, 16, 19, 21]).

To the best of our knowledge, Amarasekare [4, 5] was the first to incorporate spatial heterogeneity into models for intraguild predation. She did so through a discrete diffusion framework for three species inhabiting a network of three patches (each with a different level of resource productivity) for a total of nine ordinary differential equations that she studied numerically. She examined a number of dispersal strategies for the intraguild prey, in particular, including one which cued

upon fitness as a proxy for the balance between the need to acquire resources and the need to avoid predation.

Following [5], Ryan and Cantrell [17, 18] developed a continuous space model for intraguild predation inside a focal habitat patch, leading to a quasilinear system of parabolic partial differential equations. In this system, the resource species and the intraguild predator moved randomly inside the habitat patch via diffusion, whereas the intraguild prey's motility at a locale within the patch not only incorporated a degree of randomness but was also conditioned upon the densities of the resource species and the intraguild predator. (Spatial heterogeneity was introduced into the system through the intrinsic growth rate of the resource.) As in [5], the conditional aspect of the intraguild prey's motility depended on the balance between resource availability and predation risk involving its fitness at low abundances. When the possibility of obtaining resources outweighed potential danger from the predator, the intraguild prey's movement was close to random. On the other hand, when the situation was reversed the intraguild prey had a strong tendency to disperse away from the current risky location.

The particular model in [17] and [18] was realized as an upper triangular cross-diffusion system wherein predation was modeled vis-à-vis Holling II type functional responses and all species were subject to logistic self-regulation. Recent progress in the analysis of such systems (in particular, the results of [13]) enabled the authors to obtain global existence results sufficient for the resulting dynamical system to exhibit a compact global attractor so long as the focal habitat patch was a smooth bounded domain in \mathbb{R}^2 . The Acyclicity Theorem of Hale and Waltman [10] then leads to conditions under which the intraguild prey could persist when the tendency to move away from locales when predation risk outweighed potential for acquiring the resource was sufficiently strong.

It clearly is of interest from an ecological modeling perspective to allow for a three dimensional habitat patch, and of mathematical interest to have the patch be of an arbitrary finite dimension. However, the Gagliardo-Nirenberg type inequality based argument originating in [13] and brought to bear in [17] and [18] only works when the focal habitat patch is a bounded domain in \mathbb{R}^2 . Moreover, in [17] and [18], the conditional aspect of the intraguild prey's motility depended only on the densities of intraguild predator and the resource species and not the intraguild prey itself. In effect the intraguild prey cued upon the fitness it would have when its density was near zero. Since its persistence via the Acyclicity Theorem is predicated around its ability to increase its abundance when rare, such a limitation is not unreasonable, but it is a limitation nevertheless.

In this note, we study the closely related quasilinear parabolic system (1) and demonstrate how this model enables us to get around these obstacles by modifying the functional response to include an element of predator dependence in the functional response terms. In so doing we are assuming some degree of mutual interference in the predation process among intraguild prey relative to the resource and the intraguild predator relative to both the intraguild prey and the resource. We believe such an assumption is entirely reasonable from an ecological point of view.

The results of [13] refine the classical result of Amann [2] on global existence in quasilinear parabolic systems that asserts global existence if components of the system are asymptotically bounded in L^∞ -norm. Such bounds are simple consequences of comparison principles for single equations via upper and lower solutions

when motility is purely random, but are challenging to obtain if the motility has a nonrandom or conditional aspect to it. Le showed that if the easier condition of ultimate uniform boundedness in L^n norm, where n is the underlying spatial dimension, is met, then one can boot strap to the L^∞ bounds required to invoke the results of [2] and indeed obtain ultimate uniform bounds in a Hölder space sufficient to assert the existence of a global attractor. Gagliardo-Nirenberg identities enable one to get such bounds in L^2 norm when the focal patch is two dimensional. The inclusion of mutual interference among predators enables us to use parabolic Nash-DeGiorgi estimates instead of Gagliardo-Nirenberg estimates so as to obtain ultimate uniform boundedness of the intraguild prey density in L^n norm when the focal patch is in \mathbb{R}^n , for any $n \geq 2$. Additionally, the conditional aspect of the intraguild prey motility can now depend on the densities of all three species via its fitness. So doing provides a rather more satisfactory result from an ecological perspective.

In the remainder of this note, we present the details needed to set up the model in the case of Beddington-DeAngelis functional responses as a semi-dynamical system with a global attractor. The arguments using the Acyclicity Theorem that give sufficient conditions for the intraguild prey to persist in the system remain as in [17] and [18] and we refer the interested reader to those papers.

3. Main Results. Define, for $\lambda > 0$,

$$M_\lambda(s) = \begin{cases} d_2 & \text{for } s \geq 0, \\ -\lambda s \exp\left(\frac{d_2}{\lambda s}\right) + d_2 & \text{for } s < 0. \end{cases} \quad (5)$$

Let g be as given in (3). Then we have two different sets of assumptions for M :

(M1): M is independent of v ; that is, $M(u, v, w; \lambda) = M_\lambda(g(u, 0, w))$; or

(M2): M has dependence on v ; that is, $M(u, v, w; \lambda) = M_\lambda(g(u, v, w))$.

The assumption **(M1)** was enforced in [17, 18], where the motility of intraguild prey is conditioned on the density of resource species and intraguild predator only, but not on its own density. In contrast, **(M2)** is more realistic as the motility of intraguild prey is actually a decreasing function of its local fitness.

Definition 3.1. Let X be a complete metric space and $\gamma : [0, T) \times X \rightarrow \mathbb{R}$ where $T \in (0, \infty]$. We say that γ is *ultimately uniformly bounded with respect to X* if there exists a continuous function $C_0 : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ such that

$$|\gamma(t, x)| \leq C_0(\|x\|_X) \quad \text{for all } (t, x) \in [0, T) \times X;$$

and furthermore, if $T = \infty$ there exists a constant C_∞ such that

$$\limsup_{t \rightarrow \infty} |\gamma(t, x)| \leq C_\infty \quad \text{for all } x \in X.$$

We denote by \mathcal{P} the set of ultimately uniformly bounded functions with respect to $[W_+^{1,p}(\Omega)]^3$, where

$$W_+^{1,p}(\Omega) := \{\phi \in W^{1,p}(\Omega) : \phi \geq 0 \text{ a.e.}\}.$$

In [1, 2, 3], Amann proved existence results for a class of quasilinear parabolic equation that includes (1). In particular, [2, Theorem 1] implies that for initial conditions in $[W_+^{1,p}(\Omega)]^3$ with $p > n$ there is a unique local-in-time classical solution to (1) with a corresponding maximal interval of existence $[0, T)$ (including the possibility of $T = +\infty$). [2, Theorem 3] implies that if the L^∞ -norms of all solution

components remain bounded uniformly in $t \in [0, T)$, then the solution exists globally in time, i.e. $T = +\infty$. Also, standard comparison principles for single parabolic equations with coefficients that depend on time and space can be applied to these classical solutions to conclude that they remain non-negative in Ω for all $t \in [0, T)$ (see [14]).

We are now in a position to state our main theorems:

Theorem 3.2. *Let Ω be a smooth bounded domain in \mathbb{R}^n with $n \geq 2$ and let the initial data $(u_0, v_0, w_0) \in [W_+^{1,p}(\Omega)]^3$ with $p > n$ and, finally, let (u, v, w) be the unique local-in-time classical solution to (1) defined on some maximal existence time $[0, T)$. Assume (M1). Then this solution exists globally in time (i.e., $T = \infty$) and, furthermore, there exists a constant $0 < \gamma < 1$ such that*

$$\|u(\cdot, t)\|_{C^{1+\gamma}(\bar{\Omega})}, \|v(\cdot, t)\|_{C^{1+\gamma}(\bar{\Omega})}, \|w(\cdot, t)\|_{C^{1+\gamma}(\bar{\Omega})} \in \mathcal{P}. \quad (6)$$

In particular, the system (1) defines a semiflow on $[W_+^{1,p}(\Omega)]^3$ and this semiflow possesses a compact global attractor.

Theorem 3.3. *Let the basic assumptions be the same as Theorem 3.2. Assume (M2), and that*

$$a_3^2 h_3 \leq 4\alpha_2 \omega_2. \quad (7)$$

Then the local smooth solution (u, v, w) to (1) extends to infinity in time and fulfills the other assertions of Theorem 3.2.

4. Preliminaries.

Lemma 4.1. *There exists a constant $C_1 > 0$ such that*

$$f(x, u, v, w) \leq C_1 - \omega_1 u, \quad g(u, v, w) \leq C_1 - \omega_2 v, \quad h(u, v, w) \leq C_1 - \omega_3 w$$

for all $u, v, w \geq 0$.

Proof. For $x \in \Omega$, and $u, v, w \geq 0$, we have

$$f(x, u, v, w) \leq \sup_{\Omega} r - \omega_1 u, \quad g(u, v, w) \leq \frac{e_1}{h_1} - \mu_1 - \omega_2 v,$$

and

$$\begin{aligned} h(u, v, w) &\leq \max \left\{ \frac{e_2}{h_2}, \frac{e_3}{h_3} \right\} \frac{h_2 a_2 u + h_3 a_3 v}{1 + h_2 a_2 u + h_3 a_3 v} - \mu_2 - \omega_3 w \\ &\leq \max \left\{ \frac{e_2}{h_2}, \frac{e_3}{h_3} \right\} - \mu_2 - \omega_3 w. \end{aligned}$$

This proves the lemma. \square

Lemma 4.2. $\|u(\cdot, t)\|_{L^\infty(\Omega)}, \|w(\cdot, t)\|_{L^\infty(\Omega)} \in \mathcal{P}$.

Proof. Let

$$W_0 := \left(\max \left\{ \frac{e_2}{h_2}, \frac{e_3}{h_3} \right\} - \mu_2 \right) / \omega_3$$

so that $w(x, t)$ satisfies

$$\begin{cases} w_t - d_3 \Delta w \leq \omega_3 (W_0 - w)w & \text{in } \Omega \times (0, T), \\ \partial_\nu w = 0 & \text{on } \partial\Omega \times (0, T), \\ w(x, 0) = w_0(x) & \text{in } \Omega. \end{cases} \quad (8)$$

Next, we construct the upper solution

$$W(x, t) := \frac{W_0}{1 + \left(\frac{W_0}{\sup_{\Omega} w_0} - 1\right) e^{-\omega_3 W_0 t}},$$

which satisfies

$$\begin{cases} W_t - d_3 \Delta W = \omega_3 (W_0 - W)W & \text{in } \Omega \times (0, T), \\ \partial_\nu W = 0 & \text{on } \partial\Omega \times (0, T), \\ W(x, 0) \equiv \sup_{\Omega} w_0 \geq w_0(x) & \text{in } \Omega. \end{cases} \quad (9)$$

By comparison, $w(x, t) \leq W(x, t)$ for all $x \in \Omega$ and for all $t \in [0, T)$. Moreover, if $T = \infty$ then

$$\limsup_{t \rightarrow \infty} \left[\sup_{\Omega} w(x, t) \right] \leq \lim_{t \rightarrow \infty} \left[\sup_{\Omega} W(x, t) \right] = W_0.$$

This proves $\|w\|_{L^\infty(\Omega)} \in \mathcal{P}$. One can similarly show that $\|u\|_{L^\infty(\Omega)} \in \mathcal{P}$ and we omit the details. \square

Lemma 4.3. $\|\nabla u(\cdot, t)\|_{L^\infty(\Omega)}, \|\nabla w(\cdot, t)\|_{L^\infty(\Omega)} \in \mathcal{P}$.

Proof. From (2) and (4), we observe that for some constant C_2 independent of initial conditions,

$$|f(x, u, v, w)| \leq C_2 + \omega_1 |u| \quad \text{and} \quad |h(u, v, w)| \leq C_2 + \omega_3 |w|.$$

Therefore, Lemma 4.2 implies that $f(x, u, v, w)u \in \mathcal{P}$ and $h(u, v, w)w \in \mathcal{P}$. Applying the parabolic L^p estimates [14, Theorem 7.13] to the first equation of (1), we have for all $p > n + 2$ and all $t \in (1, T - 1)$,

$$\|u\|_{W^{2,1,p}(\Omega \times (t, t+1])} \leq C(\|u\|_{L^\infty(\Omega \times (t-1, t+1))} + \|fu\|_{L^\infty(\Omega \times (t-1, t+1))}).$$

Since the right hand side is in \mathcal{P} , one may apply the Sobolev embedding [12, p. 80, Lemma 3.3] to conclude that for some $\beta \in (0, 1)$,

$$\|u\|_{C^{1+\beta, (1+\beta)/2}(\bar{\Omega} \times [t, t+1])} \in \mathcal{P}.$$

This implies $\|\nabla u(\cdot, t)\|_{L^\infty(\Omega)} \in \mathcal{P}$.

Similarly, one may repeat the arguments to treat the third equation of (1) to obtain $\|\nabla w(\cdot, t)\|_{L^\infty(\Omega)} \in \mathcal{P}$. \square

5. Proof of Theorem 3.2. In this section, we prove Theorem 3.2. To this end, let (u, v, w) be the unique local-in-time classical solution to (1), with initial conditions in $[W_+^{1,p}(\Omega)]^3$ and with (M1) enforced.

Proposition 5.1. $\|v\|_{L^n(\Omega)} \in \mathcal{P}$.

Proof. Write the equation of v as

$$v_t - \nabla \cdot (M \nabla v) = \nabla \cdot (v M_u \nabla u + v M_v \nabla v + v M_w \nabla w) + g(u, v, w)v$$

Using Lemma 4.1, we have

$$v_t - \nabla \cdot (M \nabla v) \leq \nabla \cdot (v M_u \nabla u + v M_v \nabla v + v M_w \nabla w) + C_1 v - \omega_2 v^2 \quad (10)$$

Multiplying (10) by v^{n-1} and integrating by parts, we have

$$\begin{aligned} & \frac{1}{n} \frac{d}{dt} \int_{\Omega} v^n + \int_{\Omega} (n-1) v^{n-2} M |\nabla v|^2 + \omega_2 \int_{\Omega} v^{n+1} \\ & \leq \int_{\Omega} v^{n-1} [- (n-1) M_u \nabla u \cdot \nabla v - (n-1) M_v |\nabla v|^2 \\ & \quad - (n-1) M_w \nabla w \cdot \nabla v + C_1 v]. \end{aligned} \quad (11)$$

By **(M1)**,

$$M = M_\lambda(g(u, 0, w)) \quad \text{and} \quad M_v = 0. \quad (12)$$

Moreover, the uniform L^∞ estimates in Lemma 4.2 imply that

$$\|M_u\|_{L^\infty(\Omega)}, \|M_w\|_{L^\infty(\Omega)} \in \mathcal{P}. \quad (13)$$

Using (12), (13), the fact that $M \geq d_2 > 0$ and Lemma 4.3, we conclude that there exists $\alpha \in \mathcal{P}$ and a constant $c_0 > 0$ such that

$$\frac{d}{dt} \int_\Omega v^n + c_0 \int_\Omega v^{n-2} |\nabla v|^2 + c_0 \int_\Omega v^{n+1} \leq \alpha \int_\Omega [v^{n-1} |\nabla v| + v^n].$$

By definition of $\alpha \in \mathcal{P}$, there exists C_0, t_0 such that for all $t \geq t_0$,

$$\begin{aligned} & \frac{d}{dt} \int_\Omega v^n + c_0 \int_\Omega v^{n-2} |\nabla v|^2 + c_0 \int_\Omega v^{n+1} \\ & \leq C_0 \int_\Omega [v^{n-1} |\nabla v| + v^n] \\ & \leq \frac{c_0}{2} \int_\Omega v^{n-2} |\nabla v|^2 + \frac{C_0}{2c_0} \int_\Omega v^n + C_0 \int_\Omega v^n. \end{aligned}$$

Here the Young's inequality was used for the last inequality. Therefore,

$$\frac{d}{dt} \int_\Omega v^n + c_0 |\Omega|^{-\frac{1}{n}} \left(\int_\Omega v^n \right)^{1+\frac{1}{n}} \leq C_0 \left(\frac{1}{2c_0} + 1 \right) \int_\Omega v^n, \quad \text{for } t \geq t_0,$$

where we have used the fact that $\int_\Omega v^n \leq |\Omega|^{\frac{1}{n+1}} \left(\int_\Omega v^{n+1} \right)^{\frac{n}{n+1}}$, by Hölder's inequality. A further application of the following version of Young's inequality

$$2M \leq \epsilon M^p + \frac{p-1}{p} \left(\frac{2^p}{p\epsilon} \right)^{1/(p-1)}$$

with

$$M = \int_\Omega v^n, \quad p = 1 + \frac{1}{n}, \quad \epsilon = \frac{c_0 |\Omega|^{-1/n}}{C_0 \left(\frac{1}{2c_0} + 1 \right)},$$

yields the following Gronwall-type inequality

$$\frac{d}{dt} \int_\Omega v^n + \tilde{C}_0 \int_\Omega v^n \leq \tilde{C}_1, \quad \text{for } t \geq t_0,$$

where \tilde{C}_0, \tilde{C}_1 depend on n and $|\Omega|$ but not on initial data (u_0, v_0, w_0) . Consequently,

$$\limsup_{t \rightarrow \infty} \int_\Omega v^n \leq \left(\frac{\tilde{C}_1}{\tilde{C}_0} \right)^n,$$

where \tilde{C}_0, \tilde{C}_1 are independent of initial data (u_0, v_0, w_0) . \square

Proof of Theorem 3.2. The a priori bounds established in Lemma 4.2 and Proposition 5.1 allow us to apply [13, Theorem 2.2] or [17, Section 3.3] to conclude global existence of solutions, i.e. $T = \infty$, and moreover that (6) holds. In light of global existence of solutions, the system defines a semiflow, $\Phi(\cdot, t)$, on $[W_+^{1,p}(\Omega)]^3$ by [2, Theorem 1]. By (6), and the fact that $C^{1+\gamma}(\bar{\Omega})$ compactly embeds in $C^1(\bar{\Omega})$ which continuously embeds in $[W_+^{1,p}(\Omega)]^3$, it follows that $\Phi(\cdot, t)$ is point dissipative and asymptotically smooth. The classical result [9, Theorem 3.4.6] on the existence of compact global attractors (see also [7, Theorem 3.1] and [20, Theorem 2.30]) can then be applied. \square

6. Proof of Theorem 3.3.

Proposition 6.1. $\|v\|_{L^n(\Omega)} \in \mathcal{P}$.

Proof. Let $(u(x, t), v(x, t), w(x, t))$ be the unique classical solution to (1), with initial conditions in $[W_+^{1,p}(\Omega)]^3$ with (M2) and (7) enforced.

Claim 6.2. If (7) holds, then

$$M_v(u(x, t), v(x, t), w(x, t)) \geq 0 \quad \text{for all } x \in \Omega \text{ and } t \geq 0.$$

To see the claim, observe that

$$\begin{aligned} g_v(u, v, w) &\leq \frac{a_3 w \cdot h_3 a_3}{(1 + h_2 a_2 u + h_3 a_3 v + \alpha_2 w)^2} - \omega_2 \\ &\leq a_3^2 h_3 \left[\frac{w}{(1 + \alpha_2 w)^2} \right] - \omega_2 \\ &\leq \frac{a_3^2 h_3}{4\alpha_2} - \omega_2 \leq 0, \end{aligned} \tag{14}$$

for any $u, v, w \geq 0$. Since also $(M_\lambda)' \leq 0$ (where $M_\lambda = M_\lambda(s)$ is defined in (5)), we may then conclude that $M_v = (M_\lambda)' g_v \geq 0$. This proves Claim 6.2.

By Claim 6.2, we observe that (11) implies

$$\begin{aligned} &\frac{1}{n} \frac{d}{dt} \int_\Omega v^n + \int_\Omega (n-1)v^{n-2} M |\nabla v|^2 + \int_\Omega v^{n+1} \\ &\leq \int_\Omega v^{n-1} [-(n-1)M_u \nabla u \cdot \nabla v - (n-1)M_w \nabla w \cdot \nabla v + C_1 v]. \end{aligned} \tag{15}$$

Claim 6.3. $\|M_u\|_{L^\infty(\Omega)}, \|M_w\|_{L^\infty(\Omega)} \in \mathcal{P}$.

To see the claim, we observe that

$$g_u(u, v, w) = \frac{e_1 a_1 (1 + \alpha_1 v)}{(1 + h_1 a_1 u + \alpha_1 v)^2} + \frac{h_2 a_2 a_3 w}{(1 + h_2 a_2 u + h_3 a_3 v + \alpha_2 w)^2}.$$

By Lemma 4.2, $g_u \in \mathcal{P}$. Also, $(M_\lambda)'$ is bounded uniformly by definition (5). Hence, $M_u = (M_\lambda)' g_u \in \mathcal{P}$ as well. Similarly one can conclude that $M_w = (M_\lambda)' g_w \in \mathcal{P}$. This proves Claim 6.3.

By Claims 6.2 and 6.3 and Lemma 4.3, we may estimate (15) in a similar way as in the proof of Proposition 5.1 to conclude that $\int_\Omega v^n \in \mathcal{P}$. \square

Proof of Theorem 3.3. Theorem 3.3 is proved in exactly the same way as Theorem 3.2, by using Lemma 4.2 and Proposition 6.1 instead. \square

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REFERENCES

1. H. Amann, Dynamic theory of quasilinear parabolic equations I: Abstract evolution equations, *Nonlinear Anal.*, **12** (1988), 895–919. MR0960634
2. H. Amann, Dynamic theory of quasilinear parabolic systems III: Global existence, *Math. Z.*, **202** (1989), 219–250. MR0960634
3. H. Amann, Dynamic theory of quasilinear parabolic systems II: reaction-diffusion systems, *Differential and Integral Equations*, **3** (1990), 13–75. MR0960634
4. P. Amarasekare, Productivity, dispersal and the coexistence of intraguild predators and prey, *J. Theor. Ecol.*, **243** (2006), 121–133. Amarasekare

5. P. Amarasekare, Spatial dynamics of communities with intraguild predation: The role of dispersal strategies, *Am. Nat.*, **170** (2007), 819–831.
6. M. Arim, & P. A. Marquet, Intraguild predation: A widespread interaction related to species biology, *Ecol. Lett.*, **7** (2004), 557–564.
7. J. E. Billotti & J. P. LaSalle, Dissipative periodic processes, *Bull. Amer. Math. Soc.*, **77** (1971), 1082–1088. MR0284682
8. S. M. Durant, Living with the enemy: Avoidance of hyenas and lions by cheetahs in the Serengeti, *Behavioral Ecology*, **11** (2000), 624–632.
9. J. K. Hale, *Asymptotic Behavior of Dissipative Systems*, Math. Surveys and Monographs, Vol. 25, Amer. Math. Soc., Providence, RI, 1988. MR0941371
10. J. K. Hale & P. Waltman, Persistence in infinite-dimensional systems, *SIAM J. Math. Anal.*, **20** (1989), 388–395. MR0982666
11. R. D. Holt & G. A. Polis, A theoretical modeling framework for intraguild predation, *Am. Nat.*, **149** (1997), 745–764.
12. O. A. Ladyzhenskaya, V. A. Solonnikov, & N. N. Ural'tseva, Linear and quasi-linear equations of parabolic type, Vol. 23, Amer. Math. Soc., 1988. MR0241822
13. D. Le, Cross diffusion systems on n dimensional spatial domains, *Indiana Univ. Math. J.*, **51** (2002), 625–643. MR1911048
14. G. M. Lieberman, Second order parabolic differential equations. World Scientific Publishing Co., Inc., River Edge, NJ, 1996. MR1465184
15. E. Lucas, D. Coderre & J. Brodeur, Selection of molting and pupation sites by *Coleomegilla maculata* (Coleoptera: Coccinellidae): Avoidance of intraguild predation, *Environmental Entomology*, **29** (2000), 454–459.
16. F. Palomares & P. Ferreras, Spatial relationships between Iberian lynx and other carnivores in an area of Southwestern Spain, *Journal of Animal Ecology*, **33** (1996), 5–13.
17. D. Ryan, *Fitness Dependent Dispersal in Intraguild Predation Communities*, Ph.D thesis, University of Miami, 2011.
18. D. Ryan & R. S. Cantrell, Avoidance behavior in intraguild predation communities: A cross-diffusion model, *Discrete Contin. Dyn. Syst. A*, **35** (2015), 1641–1663. MR3285841
19. F. Sergio, L. Marchesi & P. Pedrini, Coexistence of a generalist owl with its intraguild predator: distance-sensitive or habitat-mediated avoidance?, *Animal Behavior*, **74** (2007), 1607–1616.
20. H. L. Smith & H. R. Thieme, *Dynamical systems and population persistence*, Vol. 118. Providence, RI, American Mathematical Society, 2011. MR2731633
21. C. M. Thompson & E. M. Gese, Food webs and intraguild predation: Community interactions of a native mesocarnivore, *Ecology*, **88** (2007), 334–346.

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