Appendix A: Construction and analysis of lionfish and American alligator matrix population models

Lionfish Matrix Population Model

A matrix population model for lionfish was developed by Morris et al. (2011) to investigate potential approaches for controlling the invasive species. According to the life history described in that paper, lionfish start reproducing one year after birth. Once they mature, they are very fecund, releasing a large number of eggs each month. These life history strategies make them very successful invasive species. Morris et al. (2011) took parameters from other studies (Table A.1) and produced a three-stage (larvae [age 3 d to 1 mo], juvenile [age 1 mo to 1 yr], and adult [age > 1 yr]) population matrix (Table A.2):

$$\begin{bmatrix} 0 & 0 & R_A \\ G_L & P_J & 0 \\ 0 & G_J & P_A \end{bmatrix}.$$

The time step of the model is one month.

Table A.1. Parameter values for lionfish in Morris et al. (2011).

Parameters	Value	Units
Larval mortality (M_L)	0.350	days^{-1}
Adult mortality (M_A)	0.052	months^{-1}
Juvenile mortality (M_J)	0.165	months^{-1}
Proportion female (ρ)	46%	
Larval duration (D_L)	30	days
Egg mortality (M_E)	0.310	days^{-1}
Fecundity (f)	194,577	Eggs months^{-1} female^{-1}
Egg duration (D_E)	3	days

We refer this model, with the authors' parameterization, as L1 (Table A.3). This model has several problems. First, the fertility coefficient, R_A, includes only egg survival. As the egg stage duration is only 3 days, this is insufficient; to span a 1-month time step, 27 days of either prior parent survival or subsequent larval survival needs to be included. To retain larvae in the model requires a post-breeding census formulation, with the survival of parents incorporated into the fertility term R_A. Because the fertility term included 3-day survival of eggs, we modified the fertility rate by multiplying it by the 27-day survival rate of adults $e^{-(27/30)M_A}$, assuming one month consists of 30 days. Second, P_J and G_J were calculated according to the FAS model with $T_J = 1/12$. However, according to the life history described by Morris et al. (2011), lionfish start reproducing in one year (i.e. 12 months). If so, they should spend 11 months on average in the juvenile stage rather than 12 months because individuals spend one month in the larval stage. Therefore, the coefficients in P_J and G_J were modified to 10/11 and 1/11, respectively. These corrections were incorporated into the second model (L2; Table A.2).

A remaining structural problem in the model is the age at first reproduction. According to the model, individuals spend one month in the larval stage and approximately 11 months on average in the juvenile stage. Then, they mature and reproduce. Therefore, the first offspring appears in approximately 13 months on average. One way to correct for the problem is to assume that individuals in pre-mature stage (juvenile stage) reproduce at the same time they mature when a post-breeding census model is used (e.g. Brault and Caswell 1993), by adding a fertility rate to the pre-mature stage. In model L2, $1/11$ of juveniles mature each month. Therefore, in the next model, fertility rate $\frac{1}{11}e^{-(27/30)M_J}\rho f e^{-M_E D_E}$ was added for the juvenile stage (i.e. <1,2> element of the matrix. In words, this means that $1/11$ of juveniles mature and survives over 27 days, proportion ρ of them are females, which produce f eggs, and then, those eggs survive over D_E days. We refer this model as L3.

The transition rate calculations in the above three models (L1-L3) assume proportion $1/T$ makes a transition from juvenile to adult stage when the average duration is T. This is an approximation assuming the survival rate is 1. However, in reality, some of them die before reaching the final age within the stage so that the proportion making the transition should be less than $1/T$. To account for the deaths, Crouse et al. (1987) developed a formula incorporating the survival rate. For the lionfish model, the transition rates for juvenile stage J become

$$P_J = \frac{\sum_{k=0}^{9} S_J^k}{\sum_{k=0}^{10} S_J^k} S_J,$$

$$G_J = \frac{S_j^{10}}{\sum_{k=0}^{10} S_J^k} S_j,$$

where P_J is the proportion of juveniles that survive and remain in the juvenile stage, G_J is the proportion of juveniles that survive and transition into the adult stage, and $S_j = e^{-M_J}$ is the stage specific survival rate of juveniles. The associated fertility rate for the juvenile stage is

$$R_J = \frac{S_j^{10}}{\sum_{k=0}^{10} S_J^k} e^{-(27/30)M_J} \rho f e^{-M_E D_E} .$$

We refer this model as L4.

The above transition calculation is accurate when λ is close to 1. When it is far from 1, P_J and G_J calculations need to be modified incorporating λ (Crowder et al. 1994). For the juvenile stage of lionfish,

$$P_J = \frac{\sum_{k=0}^{9}\left(S_J/\lambda\right)^k}{\sum_{k=0}^{10}\left(S_J/\lambda\right)^k} S_J \ ,$$

$$G_J = \frac{\left(S_J/\lambda\right)^{10}}{\sum_{k=0}^{10}\left(S_J/\lambda\right)^k} S_j ,$$

$$R_J = \frac{\left(S_J/\lambda\right)^{10}}{\sum_{k=0}^{10}\left(S_J/\lambda\right)^k} e^{-\left(27/30\right)M_J} \rho f e^{-M_E D_E} \ .$$

In this method, λ is needed to calculate a population matrix, but λ is often a quantity calculated from a population matrix. However, Crowder et al. (1994) have demonstrated that λ can be obtained iteratively. In this approach, λ is initially set to an arbitrary value, the population matrix with the initial λ is used to calculate a new λ, and then the population matrix is modified using the updated λ. We refer this model as L5.

Finally, the Leslie matrices (age-structured models) were constructed based on the parameters in the table (L6-L8). This model consists of 13 age classes. In this model, age class 1 has the survival rate of $e^{-M_L D_L}$, age classes 2 to 12 have the survival rate of e^{-M_J} , and age class 13 has survival rate of e^{-M_A} , which appears in the <13,13> element of the matrix. Three Leslie matrices were constructed, and they differed in the fertility coefficients. The first Leslie matrix (L6) omits the survival rates of parents in the fertility rates. Therefore, the fertility coefficients of the 12th and 13th age classes are given by $\rho f e^{-M_E D_E}$ and $\rho f e^{-M_E D_E}$, respectively. The second Leslie matrix (L7) omits reproduction term on juvenile stage so that there is only a nonzero fertility coefficient in the <1,13> element, which is given by $e^{-\left(27/30\right)M_A} \rho f e^{-M_E D_E}$. In the final Leslie matrix (L8), the fertility coefficients of the 12th and 13th age classes are given by $e^{-\left(27/30\right)M_J} \rho f e^{-M_E D_E}$ and $e^{-\left(27/30\right)M_A} \rho f e^{-M_E D_E}$, respectively.

Using the eight population matrices (Table A.3), asymptotic population growth rate λ (Figure A.1), stable stage distribution (Figure A.2), reproductive value (Figure A.3), the sensitivity (Figure A.4) and elasticity (Figure A.5) of the population growth rate to stage specific survival rate and fecundity (*f*), damping ratio (Figure A.6), and generation time (Figure A.7) were calculated. To obtain λ under L5 using the iterative method, initial λ was set to 1. Reproductive values for all models were scaled so that the reproductive value of the larval stage is 1. For calculating the stable stage distribution and sensitivity under L6-L8 for the juvenile stage, corresponding values for age-classes 2 to 12 were summed. For reproductive value for juvenile stage under L6-L8, the weighted mean of reproductive values for age classes 2 to 12, where the weight is given by their stable stage distribution, was calculated. For calculating the sensitivity of lambda under L4 and L5, numerical differentiation was used because juvenile survival S_J appears in multiple elements of the matrix under both models, and λ also appears in multiple elements under L5. In this study, generation time was defined as the mean age of mothers and calculated using the formula in Bienvenu and Legendre (2015).

Table A.2. Elements of three-stage population matrices for lionfish under L1-L5. Values are rounded values. To obtain exact values used in calculations, insert the parameter values in Table S1 into the notations shown in this table. Note $S_j = e^{-M_J}$.

	Value	Notation	Value	Notation	Value	Notation
Model	**L1**		**L2**		**L3**	
G_L	3x10^{-5}	$e^{-M_L D_L}$	3x10^{-5}	$e^{-M_L D_L}$	3x10^{-5}	$e^{-M_L D_L}$
P_J	0.777	$\left(11/12\right)e^{-M_J}$	0.771	$\left(10/11\right)e^{-M_J}$	0.771	$\left(10/11\right)e^{-M_J}$
G_J	0.071	$\left(1/12\right)e^{-M_J}$	0.077	$\left(1/11\right)e^{-M_J}$	0.077	$\left(1/11\right)e^{-M_J}$
P_A	0.949	e^{-M_A}	0.949	e^{-M_A}	0.949	e^{-M_A}
R_J	0	--	0	--	2767	$\frac{1}{11}e^{-(27/30)M_J}\rho f e^{-M_E D_E}$
R_A	35315	$\rho f e^{-M_E D_E}$	33799	$e^{-(27/30)M_A}\rho f e^{-M_E D_E}$	33700	$e^{-(27/30)M_A}\rho f e^{-M_E D_E}$
	L4		**L5**			
G_L	3x10^{-5}	$e^{-M_L D_L}$	3x10^{-5}	$e^{-M_L D_L}$		
P_J	0.818	$\frac{\sum_{k=0}^{9} S_J^k}{\sum_{k=0}^{10} S_J^k} S_J$	0.826	$\frac{\sum_{k=0}^{9} \left(S_J/\lambda\right)^k}{\sum_{k=0}^{10} \left(S_J/\lambda\right)^k} S_J$		
G_J	0.030	$\frac{S_j^{10}}{\sum_{k=0}^{10} S_J^k} S_j$	0.022	$\frac{\left(S_J/\lambda\right)^{10}}{\sum_{k=0}^{10} \left(S_J/\lambda\right)^k} S_j$		
P_A	0.949	e^{-M_A}	0.949	e^{-M_A}		
R_J	1062	$\frac{S_j^{10}}{\sum_{k=0}^{10} S_J^k} e^{-(27/30)M_J}\rho f e^{-M_E D_E}$	783	$\frac{\left(S_J/\lambda\right)^{10}}{\sum_{k=0}^{10} \left(S_J/\lambda\right)^k} e^{-(27/30)M_J}\rho f e^{-M_E D_E}$		
R_A	33700	$e^{-(27/30)M_A}\rho f e^{-M_E D_E}$	33700	$e^{-(27/30)M_A}\rho f e^{-M_E D_E}$		

Table A.3. List of models for the lionfish population and description of changes made to the original models.

Model	Description
L1	• Original three-stage model in Morris et al. (2011)

L2	• Three-stage model
	  ◦ Correction of juvenile duration
	  ◦ Incorporation of adult survival in fertility rate

L3	• Three-stage model
	  ◦ All of the corrections in L2
	  ◦ Incorporation of fertility rate of juvenile stage

L4	• Three stage model
	  ◦ All of the corrections in L3
	  ◦ Use of SAS model for calculating juvenile transition rate

L5	• Three-stage model
	  ◦ All of the corrections in L3
	  ◦ Use of AAS model for calculating juvenile transition rate

L6	• Age-structured model
	  ◦ Without survival of adults in fertility coefficient (i.e. original fertility coefficient)
	  ◦ With fertility on the last juvenile stage

L7	• Age-structured model
	  ◦ With survival of adults in fertility coefficient
	  ◦ Without fertility on the last juvenile stage (i.e. the <1,12> element is 0

L8	• Age-structured model
	  ◦ With survival of adults in fertility coefficient
	  ◦ With fertility on the last juvenile stage

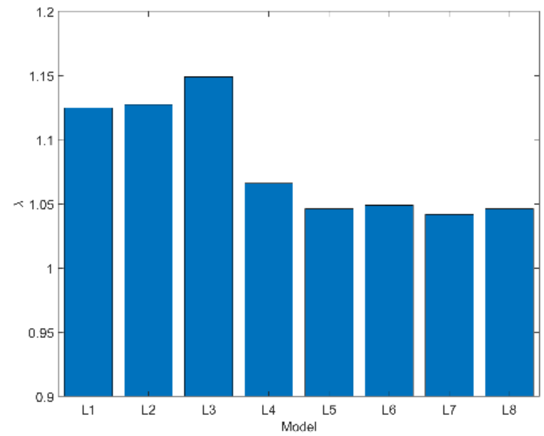

Figure A.1. Asymptotic population growth rates λ of a population under models L1-L8.

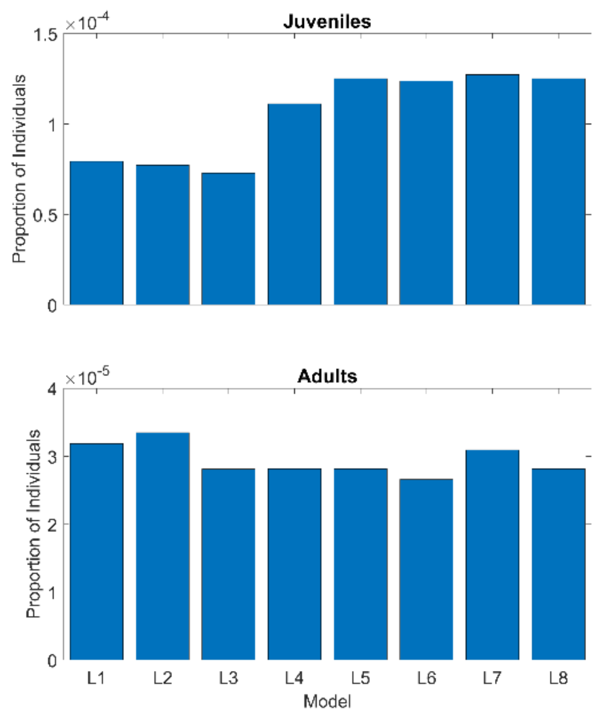

Figure A.2. Stable stage distribution of juvenile stage and adult stage of models L1-L8.

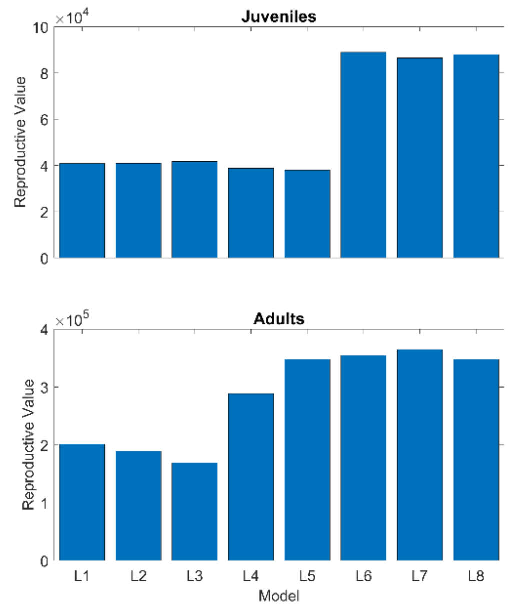

Figure A.4. Reproductive value of juveniles and adults of a population under models L1-L8

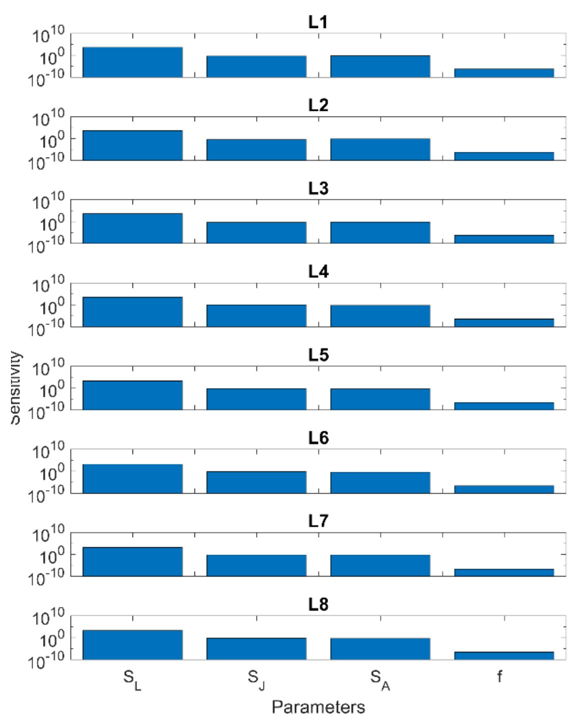

Figure A.3. Sensitivity of asymptotic population growth rate to survival and fertility rates of a population under models L1-L8.

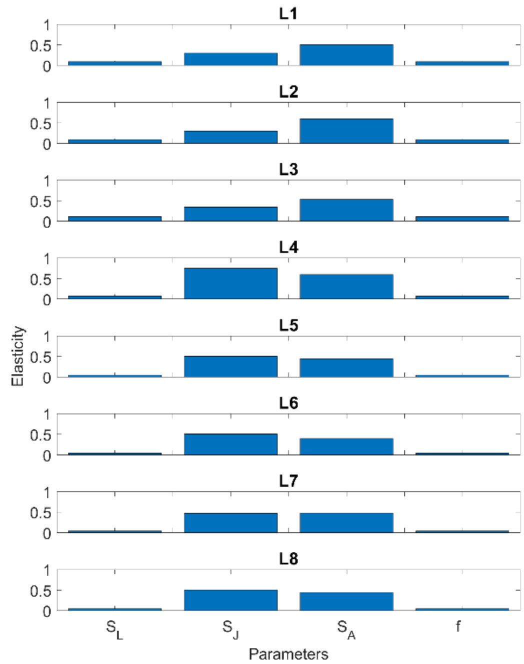

Figure A.6 Elasticity of lambda to survival and reproduction of a population under models L1-L8.

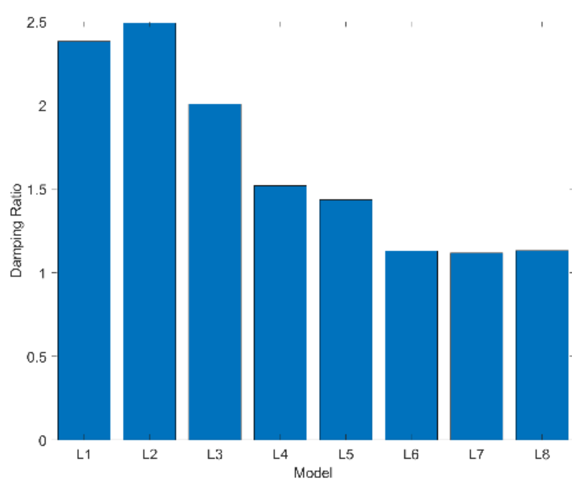

Figure A.5. Damping ratio of a population under models L1-L8.

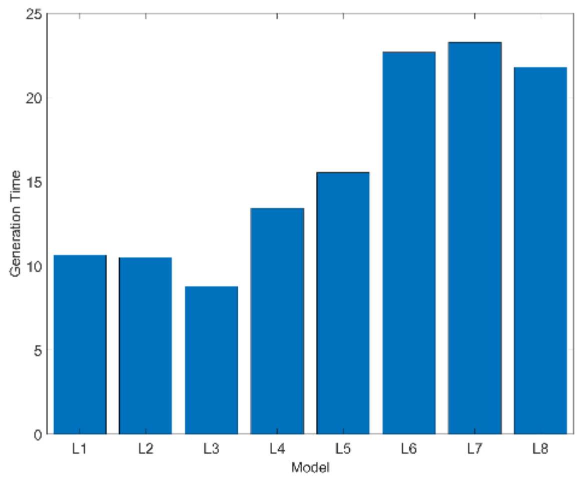

Figure A.7. Generation time of a population under models L1-L8.

Alligator Matrix Population Model

Stage-structured population matrices were constructed for two alligator populations by Duhman et al. (2014) to compare the status of northern and southern populations. Dunham et al. (2014) took parameters from other studies (Table A.4), and constructed a model consisting of five stages for each population. Because they did not have population specific estimates of survival rates, they used the same rates for both populations.

Table A.4. Parameter values for northern and southern populations of Alligator. Table was taken from Dunham et al. (2014). These values are used for our calculations.

Stage: i	Size (cm)	Stage Duration D_i (years)	Survival Rate S_i	Fecundity f (number x year^{-1})
Northern Population				
Egg: E	0	0.25	0.54 (per 3 month)	0.00
Hatchling: H	<30	1.00	0.38 (year^{-1})	0.00
Juvenile: J	30-121	7.00	0.78 (year^{-1})	0.00
Subadult: S	122-182	7.00	0.73 (year^{-1})	0.00
Adult: A	>183	>30.00	0.83 (year^{-1})	2.37
Southern Population				
Egg: E	0	0.25	0.54 (per 3 month)	0.00
Hatchling: H	<30	1.00	0.38 (year^{-1})	0.00
Juvenile: J	30-121	3.00	0.78 (year^{-1})	0.00
Subadult: S	122-182	3.00*	0.73 (year^{-1})	0.00
Adult: A	>183	>30.00	0.83 (year^{-1})	5.98

* Dunham et al. (2014) shows four years as the duration for subadult. However, we needed to change the duration to three years to make the results consistent with those presented in the paper.

Further details about the matrix models were not provided except that the Crouse *et al.* (1987) method for calculating the retention rate and transition rate in a stage-structured model was used. We constructed two matrices, one for each population to represent the original matrices described in the paper. The matrices constructed based on the descriptions in the paper resulted with a value in lambda of 0.87 for the northern population and 1.02 for the southern population, consistent with the values reported in the paper, with one modification that the duration in the subadult stage of the southern population was reduced to 3 years instead of 4 years. With this modification, both matrices also gave almost the same reproductive values and stable stage distributions listed in the paper. The matrix models in Dunham et al. (2014) were five-stage models (*E*: egg; *H*: hatchling; J: juvenile; S: subadult; and A: adult) where a population matrix is given as:

$$\begin{pmatrix} 0 & 0 & 0 & 0 & R_A \\ G_E & 0 & 0 & 0 & 0 \\ 0 & G_H & P_J & 0 & 0 \\ 0 & 0 & G_J & P_S & 0 \\ 0 & 0 & 0 & G_S & P_A \end{pmatrix}.$$

The values for these elements are shown in Table A.5. We refer the original matrices for northern and southern populations as AN1 and AS1, respectively (Table A.6).

One of the major problems in the construction of the matrices was that, although the models assumed a post-breeding census, the fecundity terms did not include adult or egg survival. To correct for this, we reduced the number of stages from five to four so that the first stage is hatchling, and the fertility rate was modified to include the survival rates of the egg (s_E) over three months and adult (s_A) over 9 months as $R_A = s_A^{9/12} f s_E$ where f is the product of mean clutch size, sex ratio, and percent of females breeding. In addition, we also incorporated the fertility rate for the subadult stage as

$$R_S = \frac{s_S^6}{\sum_{k=0}^{6} s_S^k} s_S^{9/12} f s_E .$$

Incorporating the fertility rate for the subadult stage, we assumed that individuals remain in the juvenile stage for seven years on average, but when they transition into adult stage, they also reproduce. A resulting population matrix is given as

$$\begin{pmatrix} 0 & 0 & R_S & R_A \\ G_H & P_J & 0 & 0 \\ 0 & G_J & P_S & 0 \\ 0 & 0 & G_S & P_A \end{pmatrix}.$$

In this matrix, other elements (i.e. P's and G's) remain the same except their locations in the matrix were changed as shown in the matrix above. We refer the modified matrices for the northern and southern populations as AN2 and AS2, respectively.

As discussed with the lionfish model, the method of Crouse *et al.* (1987) assumes that population growth rate λ to be 1. When the growth rate is far from 1, the survival rate in the transition calculation needs to be discounted with λ. The model with λ incorporated into the transition calculations (which affect P_J, G_J, P_S, G_S, and R_S) are referred as AN3 and AS3 for northern and southern populations, respectively.

Finally, three Leslie matrices were constructed for northern and southern populations using the same survival rate as the stage-structured models. The Leslie matrices for the northern population (AN4-AN6) consists of 16 age classes, and that for southern population (AS4-AS6) consists of eight age classes. Under models AN4 and AS4, the parent survival rate was omitted in fertility rate so that adult stage and the last age class of subadult stage have positive fertility rate $R_i = s_i^{9/12} f s_E$ where i denotes the age class of parents reproducing. Under models AN5 and AS5, the fertility rate of the last age class of subadult was omitted so that only the last age class has fertility rate $R_i = s_i^{9/12} f s_E$. Finally, under models AN6 and AS6, both adult stage and the last age class of subadult stage have fertility rate $R_i = s_i^{9/12} f s_E$.

In total, twelve models were constructed with AN1-AN6 corresponding to the northern population and AS1-AS6 corresponding to the southern population. Elements of the population matrices for the six stage-structured populations are shown in Table A4.

Using the twelve population matrices, asymptotic population growth rate λ (Figure A.8), stable stage distribution (Figure A.9), reproductive value (Figure A.10), the sensitivity (Figure A.11) and elasticity (Figure A.12) of the population growth rate to stage specific survival rate and fecundity (*f*), damping ratio (Figure A.13), and generation time (Figure A.14) were calculated. To obtain λ under AN3 and AS3 using the iterative method, initial λ was set to 1. Reproductive values for all models were scaled so that the reproductive value of the hatchling stage is 1. For calculating the stable stage distribution and sensitivity under AN4-AN6 and AS4-AS6 for the hatchling and subadult stages, corresponding values for age-classes were summed. Similarly, reproductive values for these stages under AN4-AN6 and AS4-AS6 were calculated by taking the weighted mean of reproductive values for corresponding age classes, where the weight is given by their stable stage distribution. For calculating the sensitivity of lambda under all stage-structured models (i.e. except AN4-AN6 and AS4-AS6), numerical differentiation was used because juvenile survival S_J appears in multiple elements of these matrices, and λ appears in multiple elements under AN3 and AS3. In this study, generation time was defined as the mean age of mothers and calculated using the formula in Bienvenu and Legendre (2015).

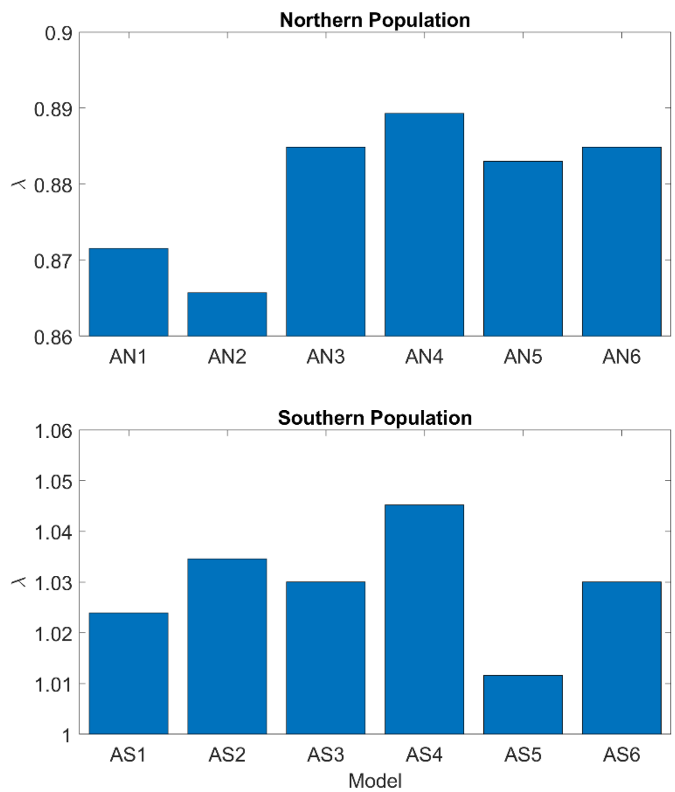

Figure A.8 Asymptotic population growth rates of populations under A1-A12.

Table A.5. Elements of matrix population models for northern and southern alligator populations. Values are rounded values. To obtain exact values used in calculations, insert the parameter values in Table S3 into the notations shown in this table.

	North	**South**	**Notation**	**North**	**South**	**Notation**	**North**	**South**	**Notation**
Model	**AN1**	**AS1**	**AN1 & AS1**	**AS2**	**AS2**	**AN2 & AS2**	**AN3**	**AS3**	**A3N & AS3**
G_E	0.54	0.54	s_E	--	--	--	--	--	--
G_H	0.38	0.38	s_H	0.38	0.38	s_H	0.38	0.38	s_H
P_J	0.73	0.58	$\frac{\sum_{k=0}^{D_H-2} s_H^k}{\sum_{k=0}^{D_H-1} s_H^k} s_H$	0.73	0.58	$\frac{\sum_{k=0}^{D_H-2} s_H^k}{\sum_{k=0}^{D_H-1} s_H^k} s_H$	0.71	0.59	$\frac{\sum_{k=0}^{D_H-2} \left(s_H/\lambda\right)^k}{\sum_{k=0}^{D_H-1} \left(s_H/\lambda\right)^k} s_H$
G_J	0.047	0.20	$\frac{s_H^{D_H-1}}{\sum_{k=0}^{D_H-1} s_J^k} s_H$	0.047	0.20	$\frac{s_H^{D_H-1}}{\sum_{k=0}^{D_H-1} s_J^k} s_H$	0.074	0.19	$\frac{\left(s_H/\lambda\right)^{D_H-1}}{\sum_{k=0}^{D_H-1} \left(s_H/\lambda\right)^k} s_H$
P_S	0.70	0.56	$\frac{\sum_{k=0}^{D_H-2} s_S^k}{\sum_{k=0}^{D_H-1} s_S^k} s_S$	0.70	0.56	$\frac{\sum_{k=0}^{D_H-2} s_S^k}{\sum_{k=0}^{D_H-1} s_S^k} s_S$	0.68	0.56	$\frac{\sum_{k=0}^{D_S-2} \left(s_S/\lambda\right)^k}{\sum_{k=0}^{D_S-1} \left(s_S/\lambda\right)^k} S_S$
G_S	0.034	0.17	$\frac{s_S^{D_S-1}}{\sum_{k=0}^{D_S-1} s_S^k} s_S$	0.034	0.17	$\frac{s_S^{D_S-1}}{\sum_{k=0}^{D_S-1} s_S^k} s_S$	0.054	0.17	$\frac{\left(s_S/\lambda\right)^{D_S-1}}{\sum_{k=0}^{D_S-1} \left(s_S/\lambda\right)^k} s_S$
P_A	0.83	0.83	s_A	0.83	0.83	s_A	0.83	0.83	s_A
R_S	0	0	0	0.046	0.600	$\frac{s_S^6}{\sum_{k=0}^{6} s_S^k} s_S^{9/12} f s_E$	0.075	0.579	$\frac{\left(s_S/\lambda\right)^{D_S-1}}{\sum_{k=0}^{D_S-1} \left(s_S/\lambda\right)^k} s_S^{9/12} f s_E$
R_A	2.37	5.98	f	1.11	2.81	$s_A^{9/12} f s_E$	1.11	2.81	$s_A^{9/12} f s_E$

Table A.6. List of models for American alligators and description of changes made to the original models.

Model		Description
Northern Population	Southern Population	
AN1	AS1	• Original five-stage model in Dunham et al. (2014)

AN2	AS2	• Four-stage model (hatchling, juvenile, subadult, and adult)
		    • Incorporation of survival rate into fertility rate of adult stage
		    • Addition of fertility rate to subadult stage

AN3	AS3	• Four-stage model
		    • All of the corrections made in A2
		    • Calculation of juvenile transition rates using AAS model

AN4	AS4	• Age-structured model
		    • Without survival of adults in fertility coefficient (i.e. original fertility coefficient)
		    • With fertility on the last subadult stage

AN5	AS5	• Age-structured model
		    • With survival of adults in fertility coefficient
		    • Without fertility on the last subadult stage (i.e. the <1,12> element is 0

AN6	AS6	• Age-structured model
		    • With survival of adults in fertility coefficient
		    • With fertility on the last subadult stage

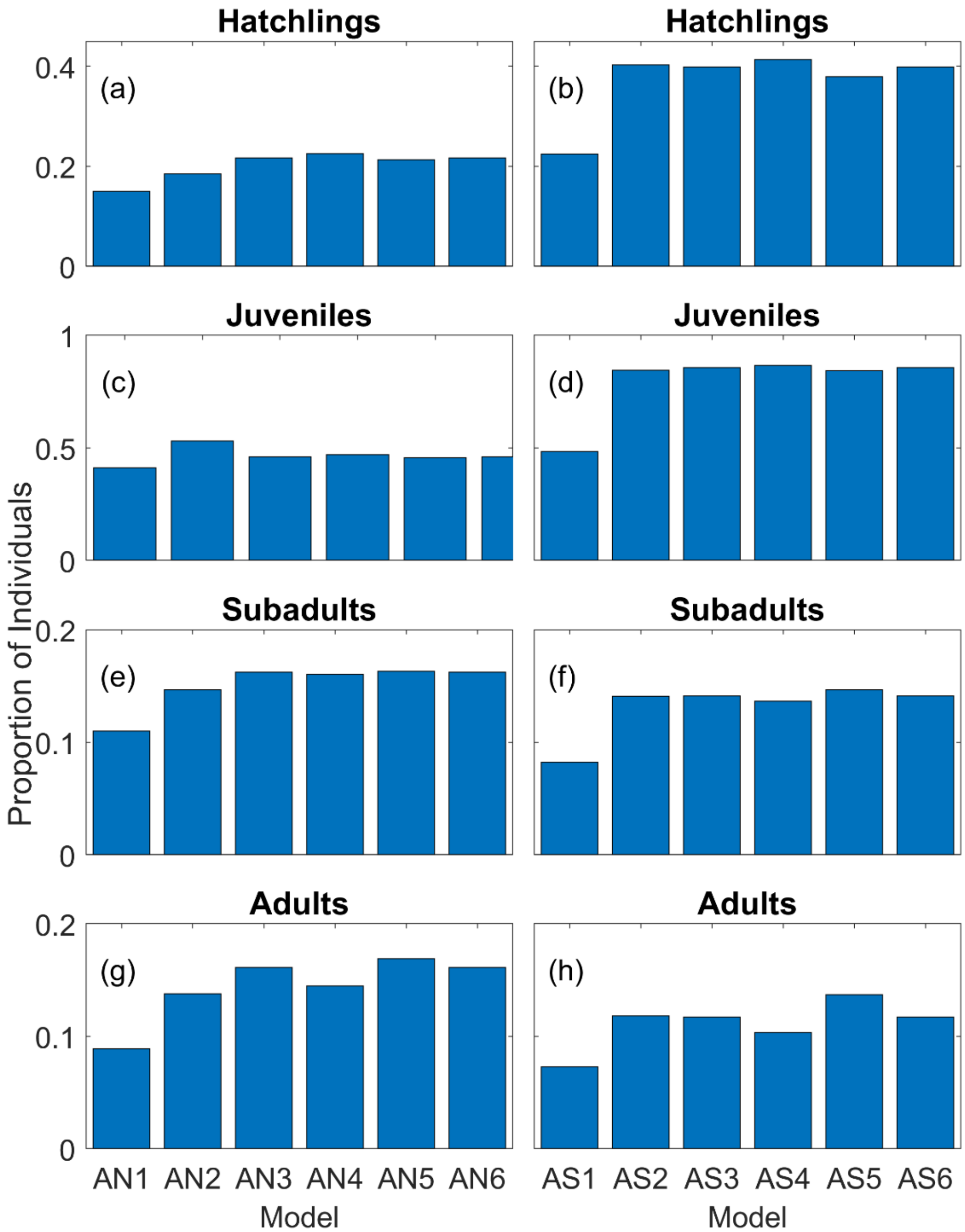

Figure A.9. Stable stage distribution of hatchling, juvenile, subadult, and adult stages under the six different models. The panels on the left are for northern population, and the panels on the right are for southern populations.

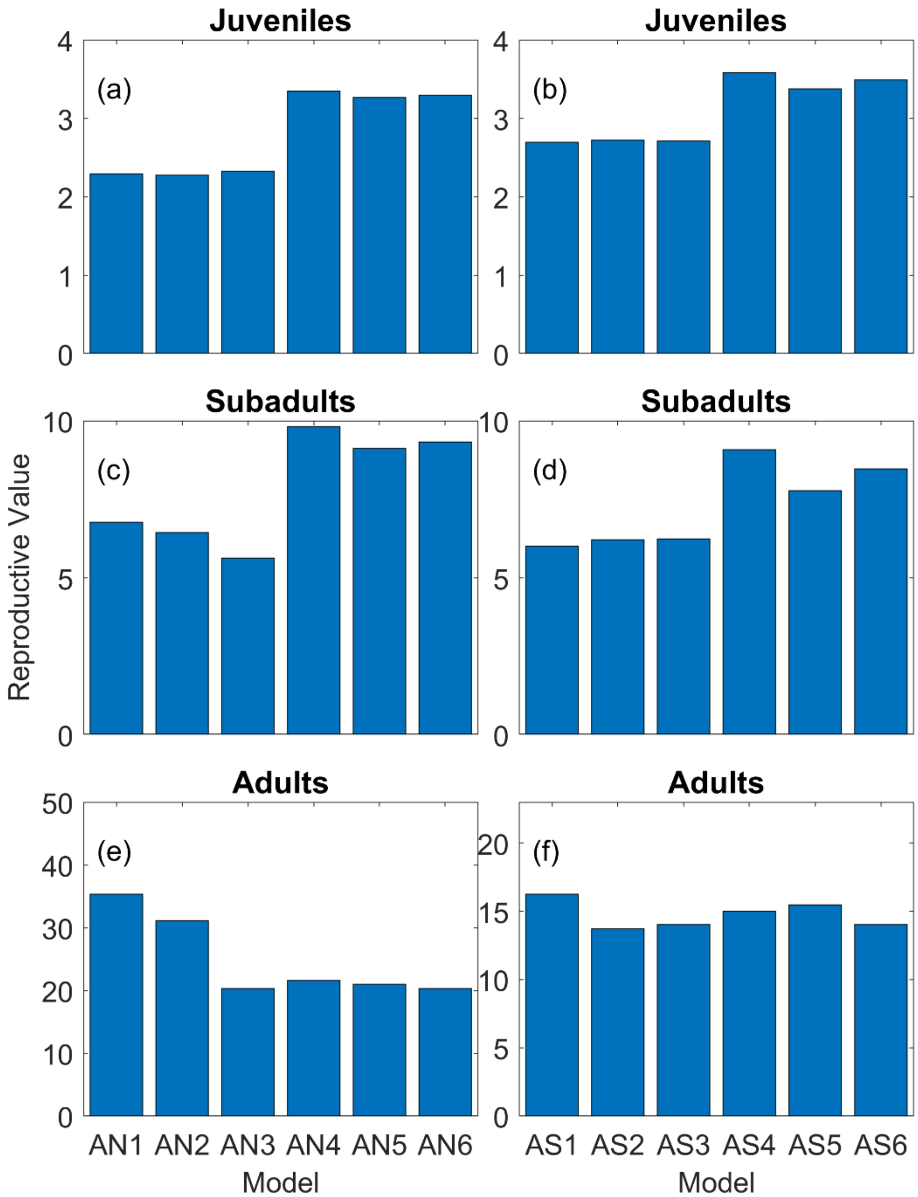

Figure A.10. Reproductive value of juveniles, subadults and adults under the six different models. The panels on the left are for northern population, and the panels on the right are for southern populations.

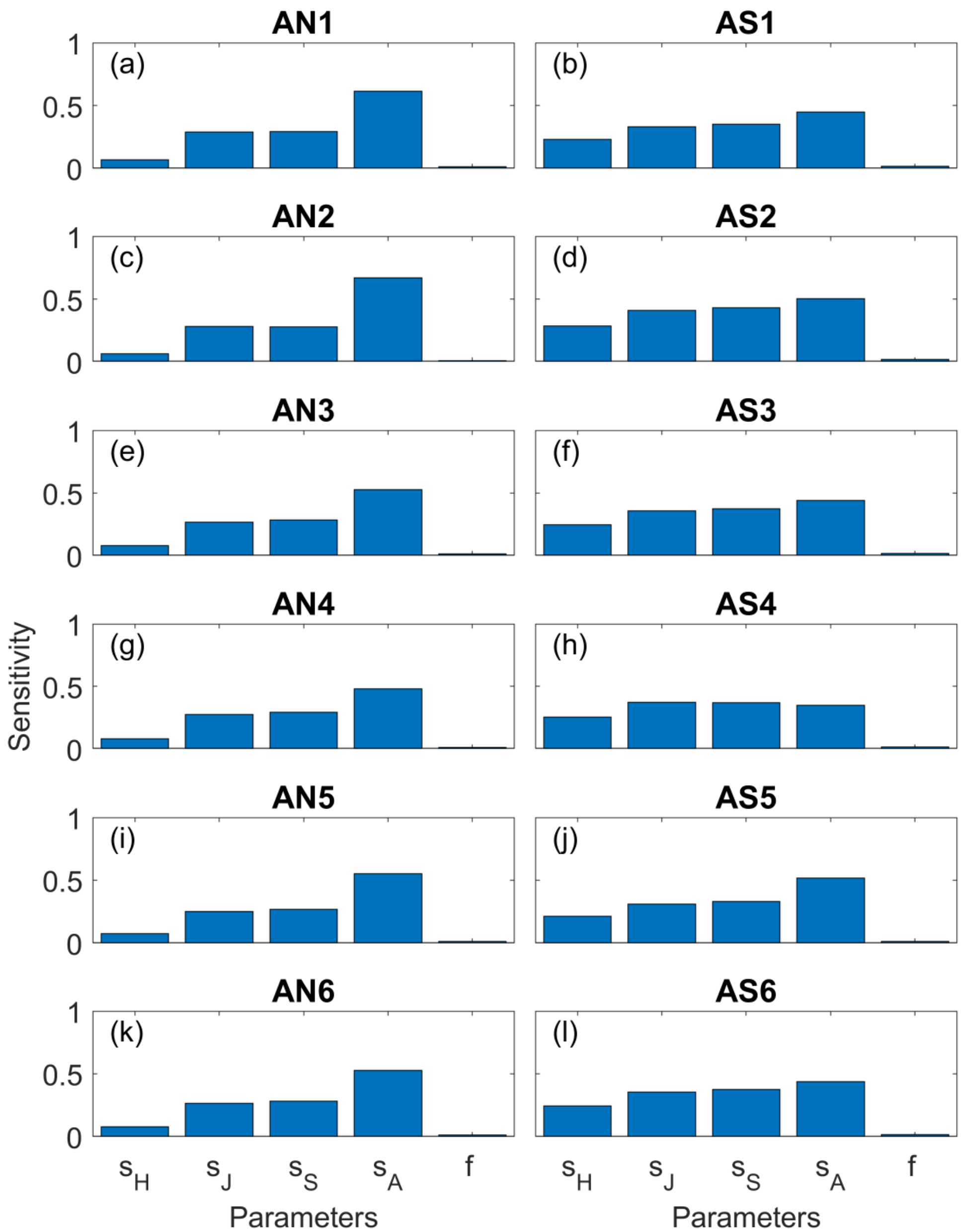

Figure A.11. Sensitivity of lambda to stage-specific survival and fecundity. H: hatchling, J: juvenile, S: subadults, A: adults. The panels on the left are for northern population, and the panels on the right are for southern populations.

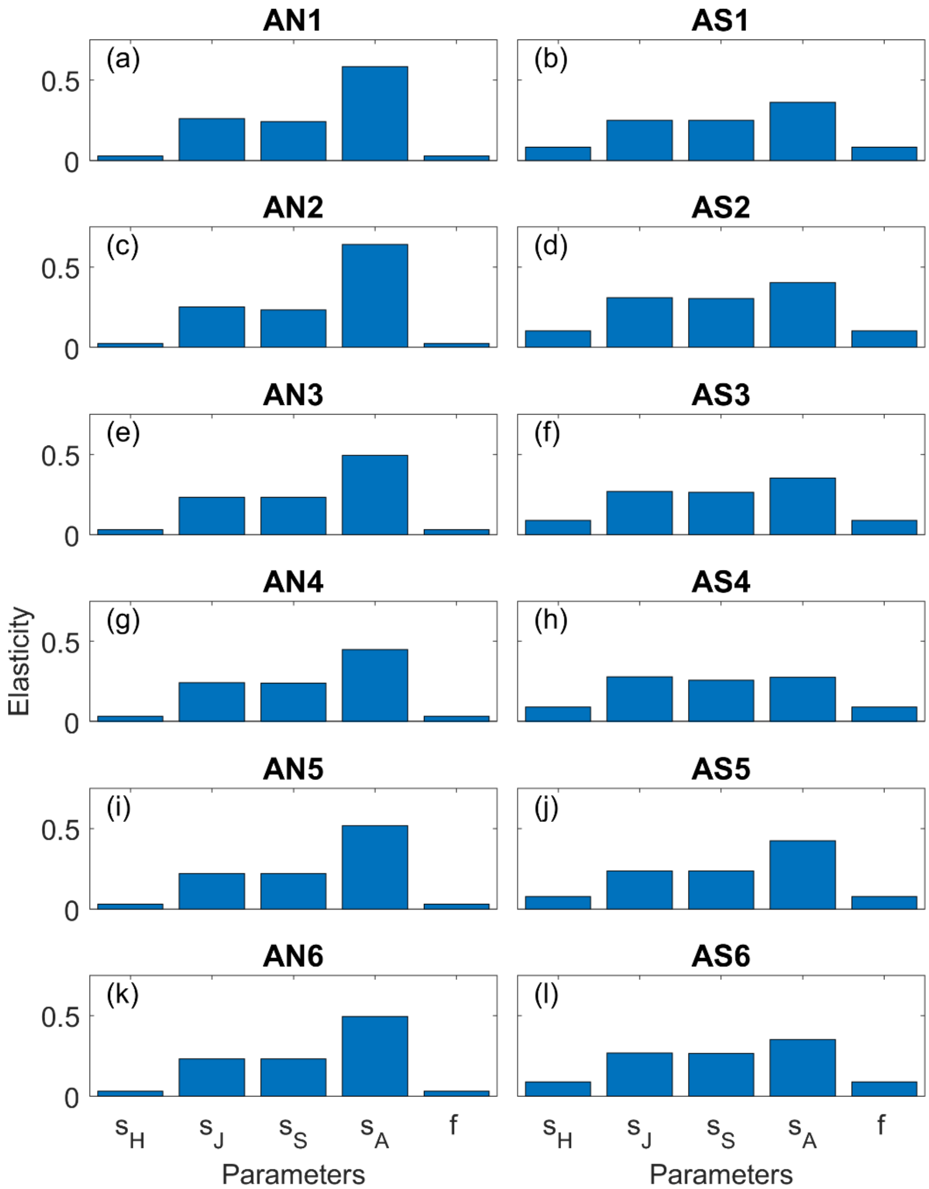

Figure A.12. Elasticity of lambda to stage-specific survival and fecundity. H: hatchling, J: juvenile, S: subadults, A: adults. The panels on the left are for northern population, and the panels on the right are for southern populations.

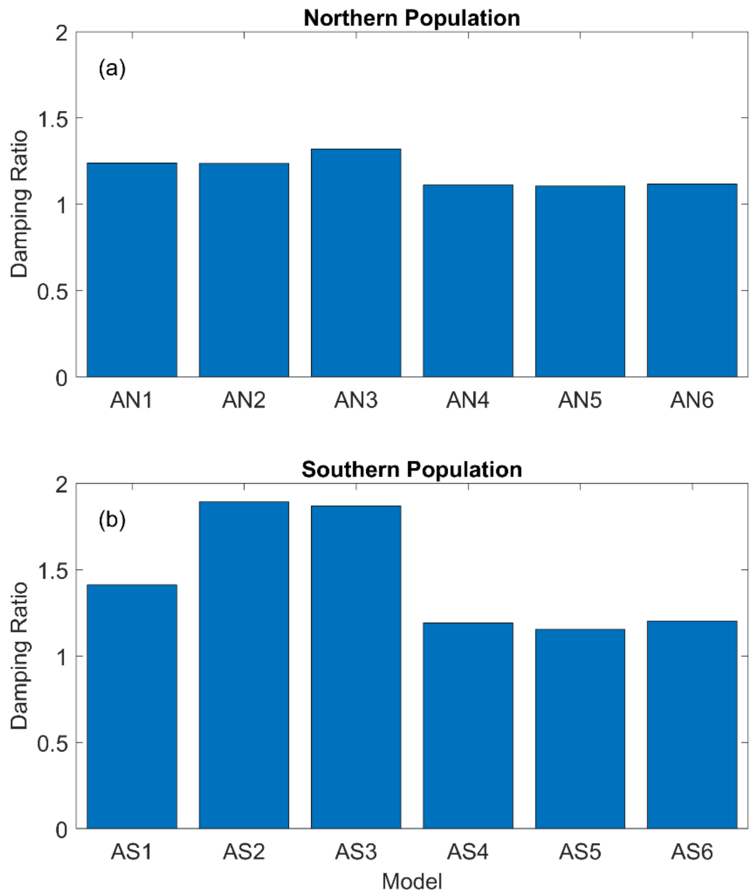

Figure A.13. Damping ratio of populations under six different models. (a) Northern population and (b) Southern population.

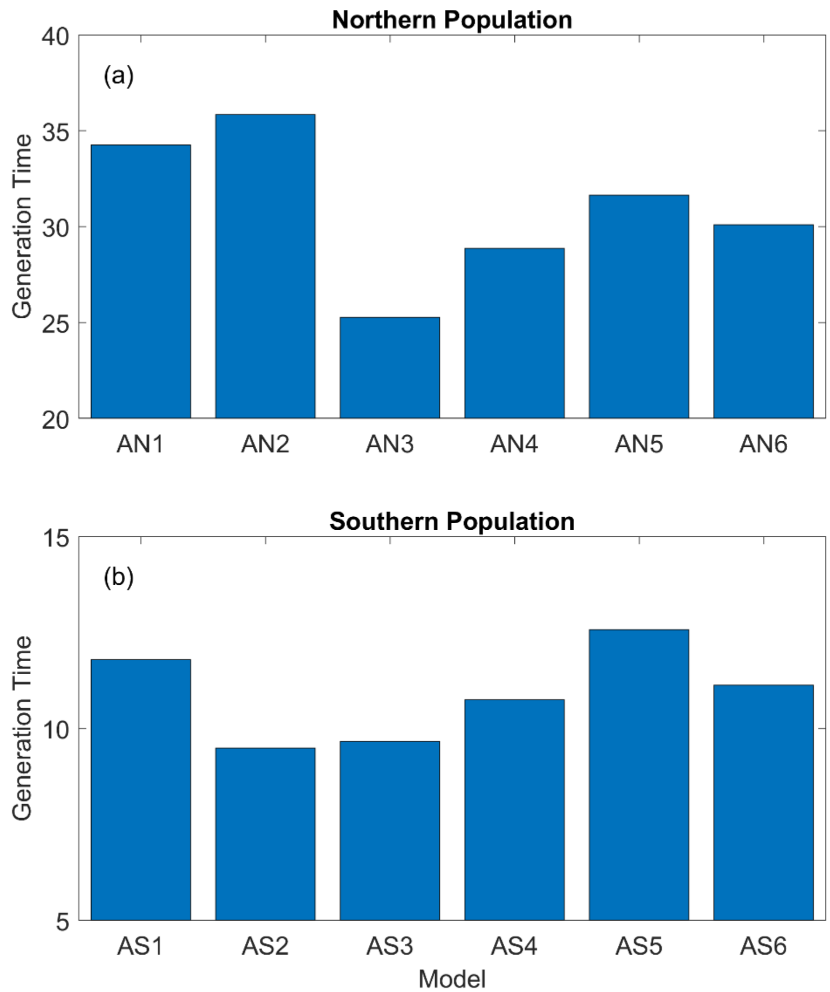

Figure A.14. Generation time of populations under six different models. (a) northern population and (b) southern population.

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