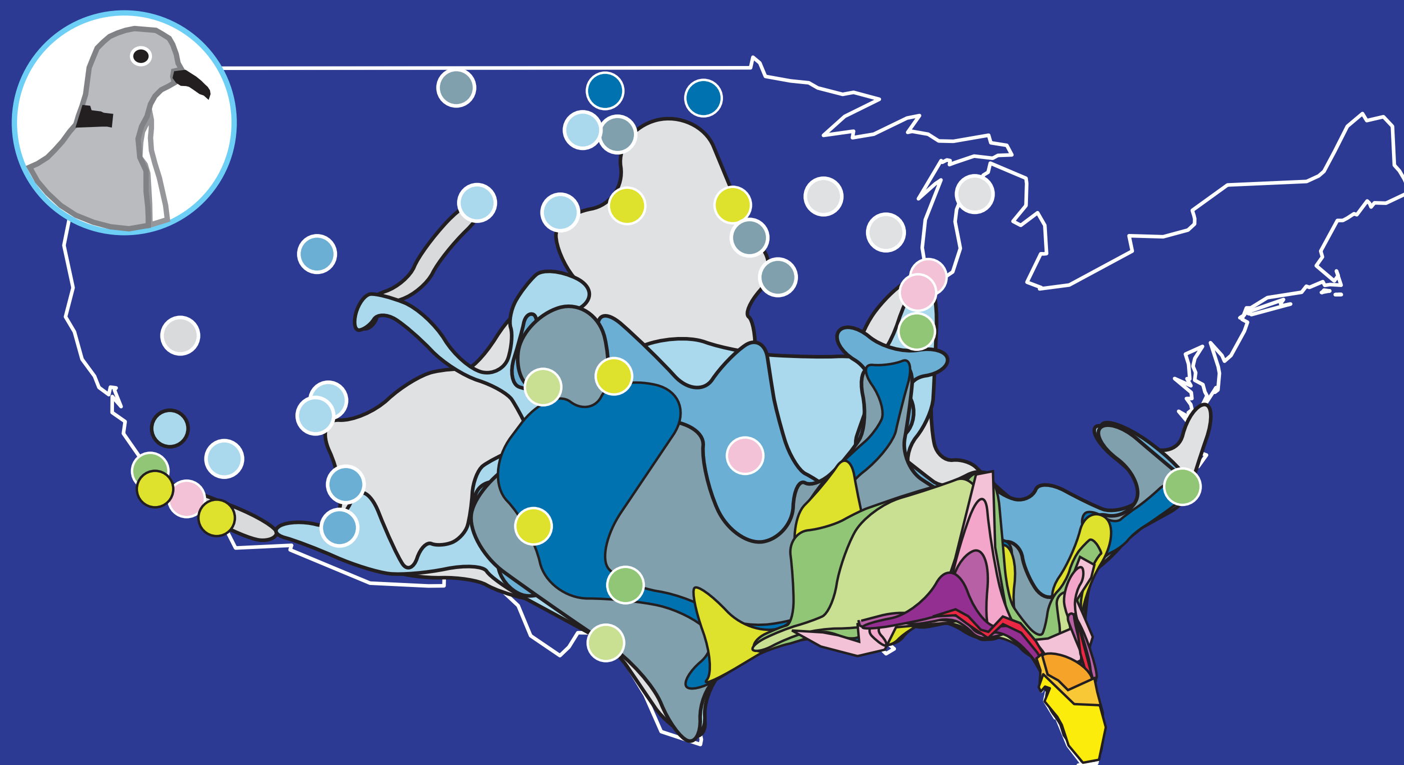
Using Integro-Difference Equations To Model The Effect Of Growing Season Length On The Spread Of The Eurasian Collared Dove In North America



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Talk Outline

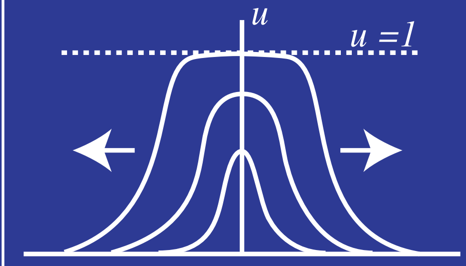
- Review of Invasion Modeling Approaches
- The Veit-Lewis 2-Stage Model
- Invasion Dynamics of the Eurasian Collared-Dove
- Spatially-Dependent-Breeding Model
- Results & Model Comparison
- Conclusions
- Acknowledgements

Review of Modeling Approaches

Reaction–Diffusion models (RD)

$$\frac{\partial N}{\partial t} = rN + D\left[\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2}\right]$$

- Continuous time, continuous space
- For continuous growth and dispersal
- Example: the Fisher equation:



$$\frac{\partial u}{\partial t} = ru(1-u) + D\frac{\partial^2 u}{\partial x^2}$$

Integro–Difference Equations (IDE)

- Discrete time, continuous space:
- For discrete growth and dispersal stages
- aka discrete time spatial contact model
- Shown to improve prediction of the speed of the wave front (Kot 2003,Canadian Applied Math Quarterly) (Kot, 2003. *Can Appl Math Q.*)

$$N_{t+1}(x) = \int_a^b k(x,y) f(N_t(y))\,dy$$

Less Common Approaches

- Hierarchical Bayes (RD with spatial heterogeneity) e.g. Wikle, C.K. 2003. *Ecology* **84**:1382
- Individual–Based Models e.g. Grimm V. et al. 2005. *Science* **310**:987

Veit-Lewis 2-Stage Model

Veit, R. and M. Lewis. 1996 *The American Naturalist* 148:255-274

Invasion model for house finch in North America

Separate Stages for Growth and Dispersal

$$N_{t+1}(x) = s(1-\rho_a)N_t(x) + (1-\rho_j)f[N_t(x)]$$
$$+ \int_{-\infty}^{+\infty} \kappa(|x-y|)s\rho_a N_t(y)dy$$
$$+ \int_{-\infty}^{+\infty} \kappa(|x-y|)\rho_j f[N_t(y)]dy$$

- Dispersal kernel = Weibull distribution (fit using banding data)
- Density-dependent dispersal rates
- Uses different dispersal probabilities for adults and juveniles
- Predicts the density of birds at point x, after the dispersal stage

Veit-Lewis 2-Stage Model

Popuation Growth Stage

$$N_{t+1} = sN_t + \frac{cN_t^2}{r + 2N_t + \frac{N_t^2}{\delta}}$$

where: $r = \dfrac{4}{\sigma T}$

c = average no. offspring per breeding pair that survive to $t + 1$

s = annual survival rate

δ = density of nest sites

σ = rate of pair formation

T = length of breeding season

Growth Function Assumptions

- 1:1 sex ratio
- Offspring born in year t can breed in t+1
- Number broods uniform across space and time

Veit-Lewis 2-Stage Model

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T = length of breeding season

Density of Potential Breeders

for fixed time interval T

$$P = \frac{N_t^2}{\frac{4}{(\sigma\tau)} + 2N_t}$$

σ = *rate of pair formation*

τ = *particular time inteval*

Generates weak Allee effect.

Density of Actual Breeding Pairs

Beverton-Holt stock recruitment function

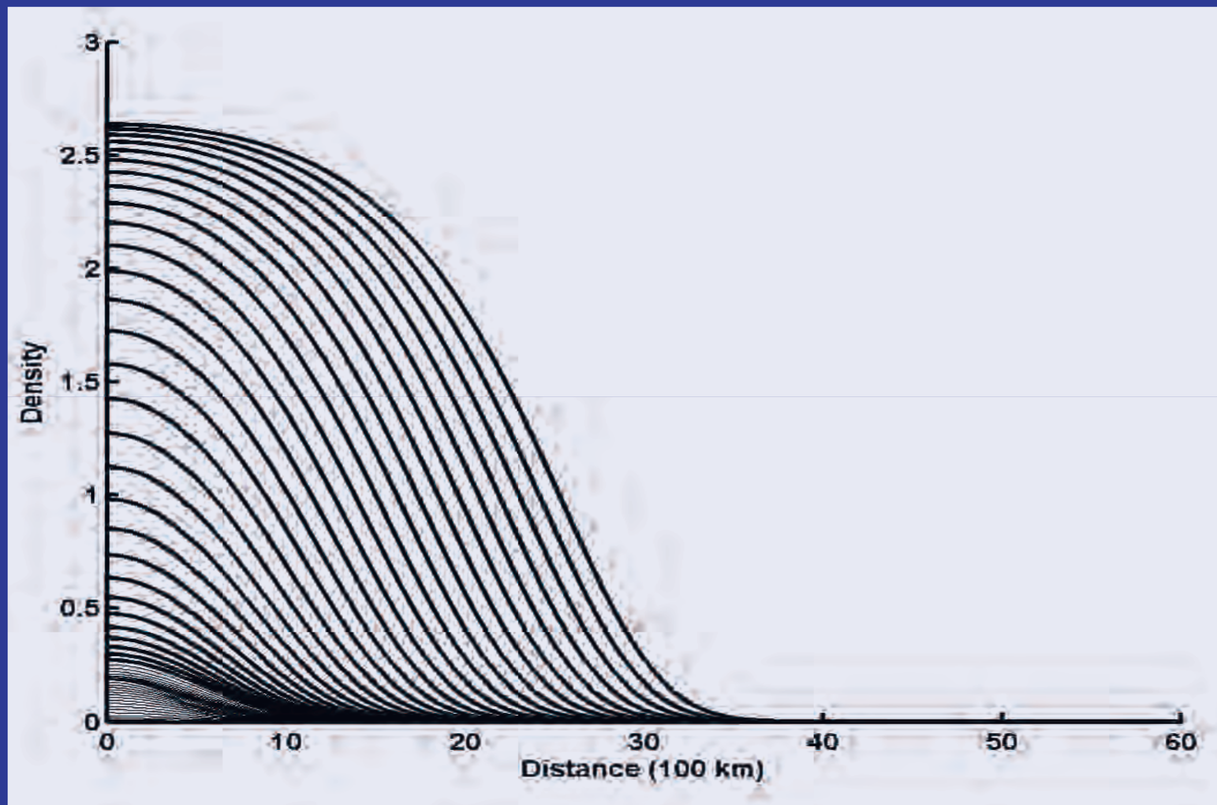
$$H = \frac{P}{1 + \frac{P}{\delta}}$$

Growth Function Assumptions

- 1:1 sex ratio
- Offspring born in year t can breed in t+1
- Number broods uniform across space and time

Veit-Lewis 2-Stage Model

Shape of Wave Front



- constant or accelerating wave front, depending on dispersal kernel
- height of curve set by carrying capacity

Invasion Dynamics of the Collared Dove

Portrait of a successful invader

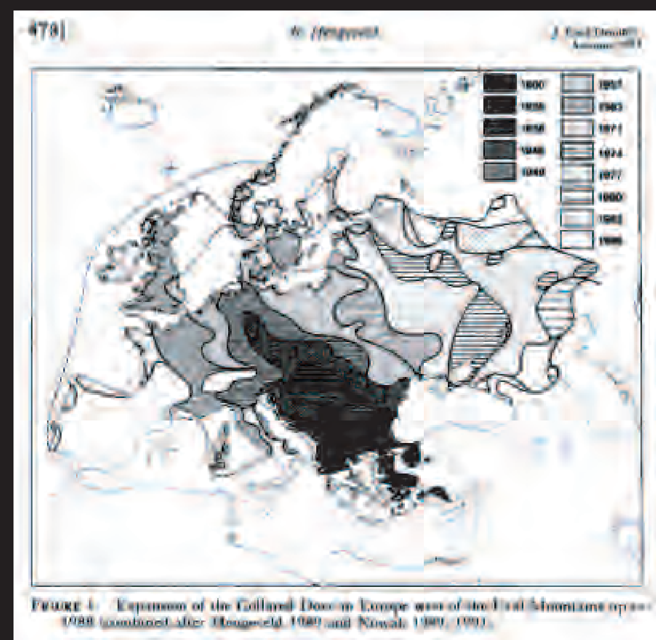
Streptopelia decaocto

- Aggressive toward other birds
- Multi-Brooded (up to 6 clutches per year)
- Single pair can have multiple active nests
- Population growth facilitated by human activities
- Long-distance disperser

Photo by PETER WALLACK

European Invasion

- Historic range in India, Sri Lanka, Myanmar
- Expanded into Turkey & Balkans (1600s)
- Began expansion into Europe in 1928
- Occupied Europe, Britain, Scandinavia by 1960s
- Invasion routes tend to follow coastlines, valleys



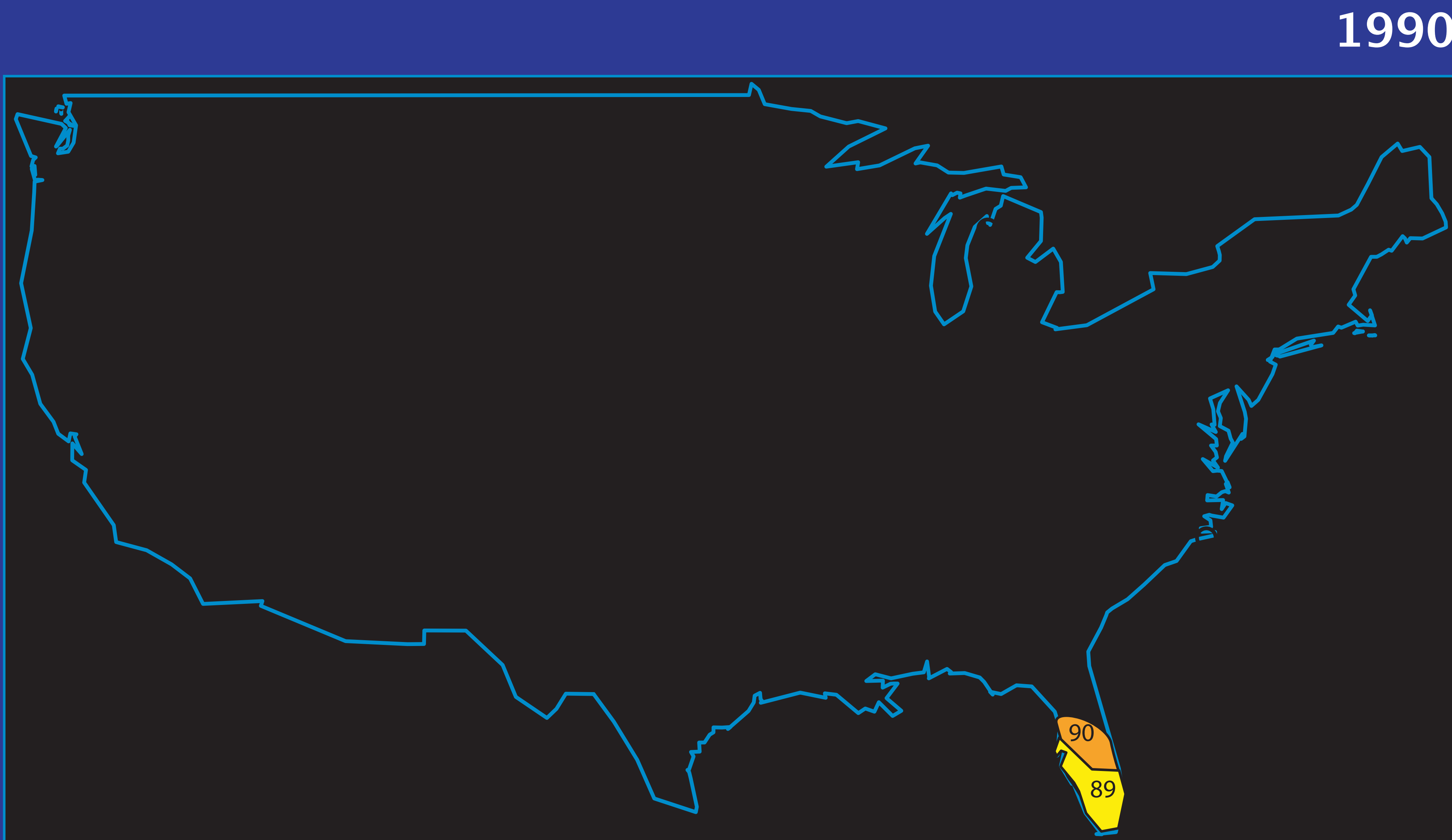
Robert Hengeveld 1993
J. Field Ornithology 64:477-489.

Winter Distribution 1989–2004

1989

SOURCE: Audubon Christmas Bird Count

Winter Distribution 1989–2004



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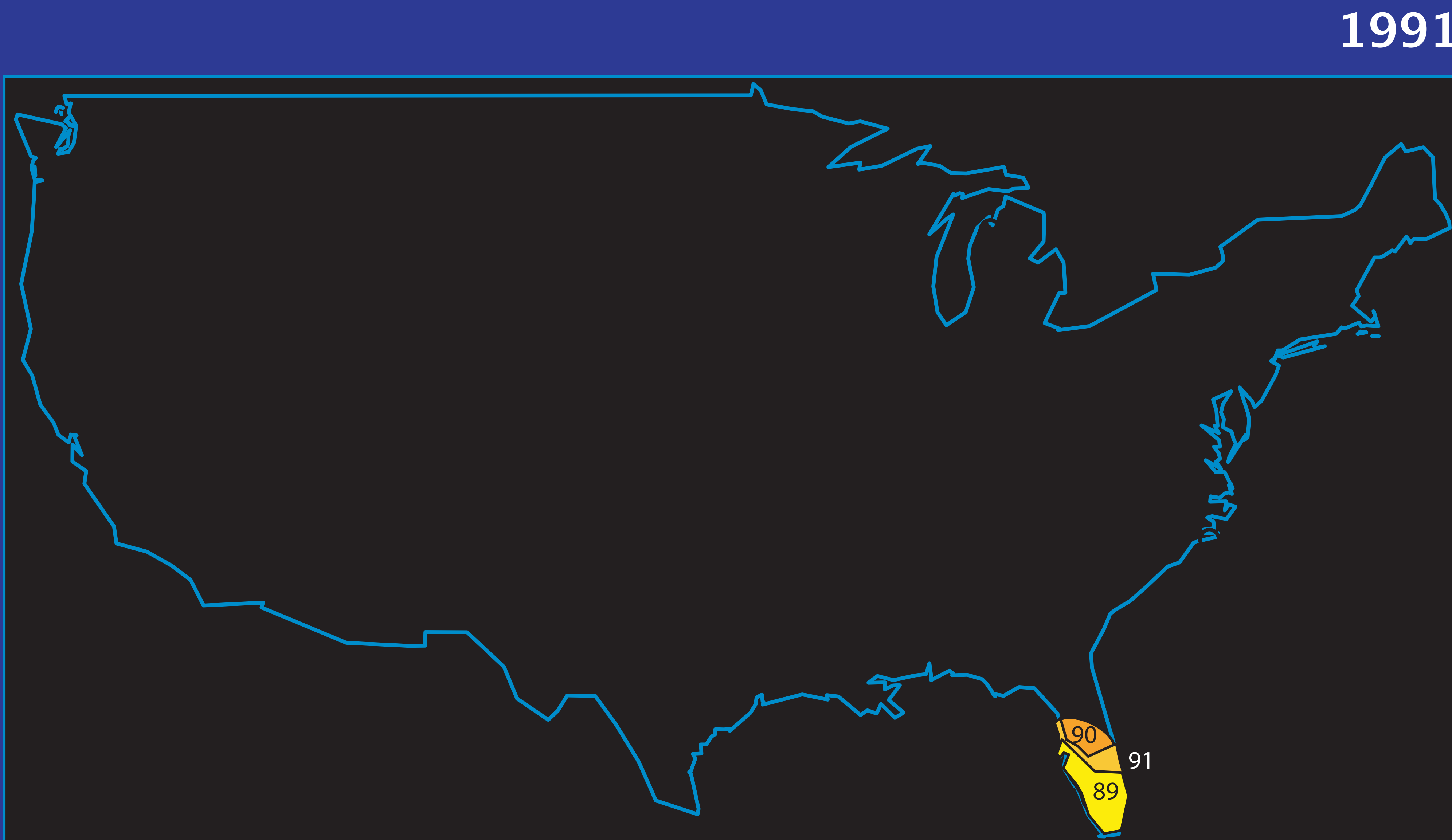

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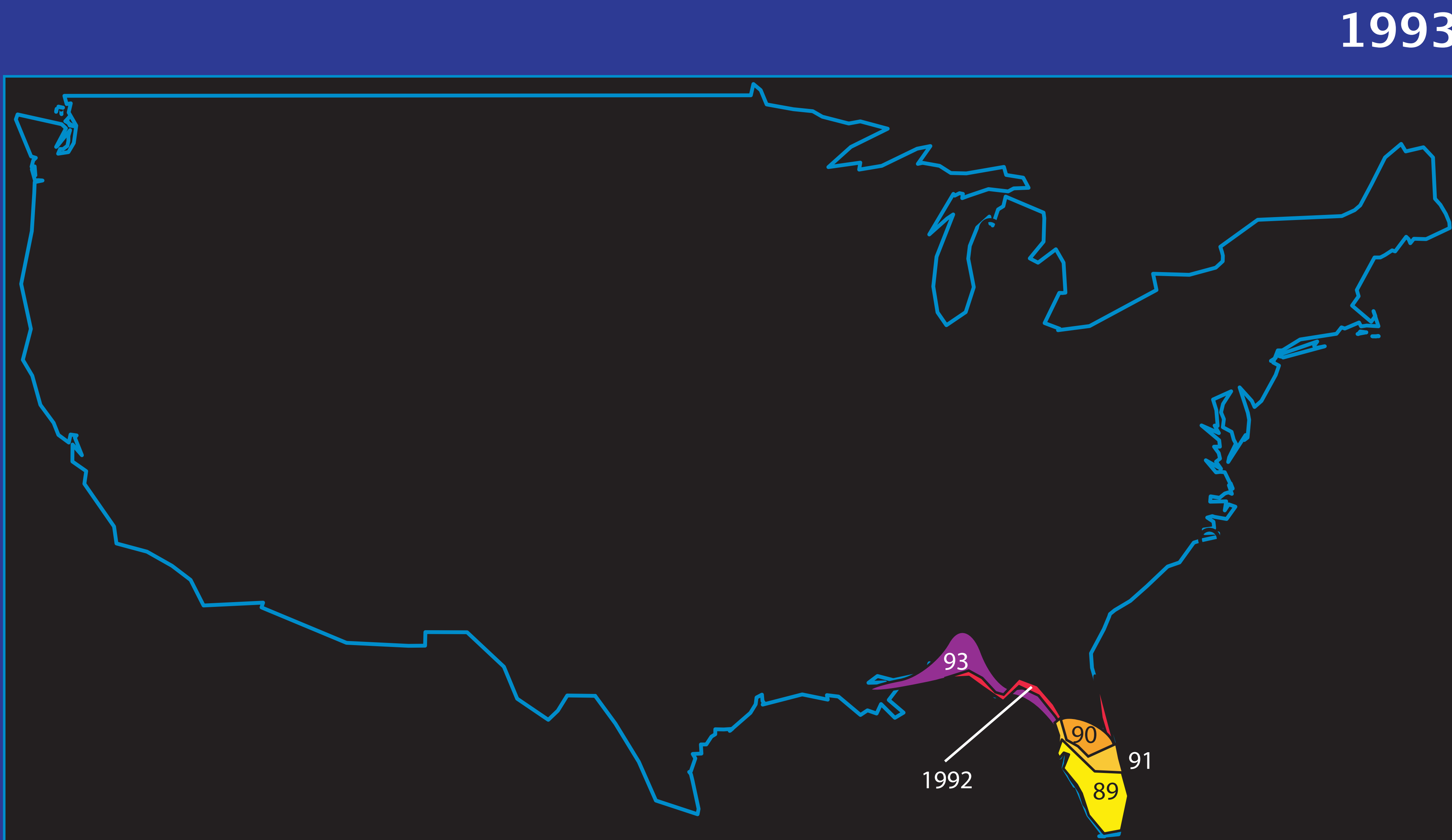
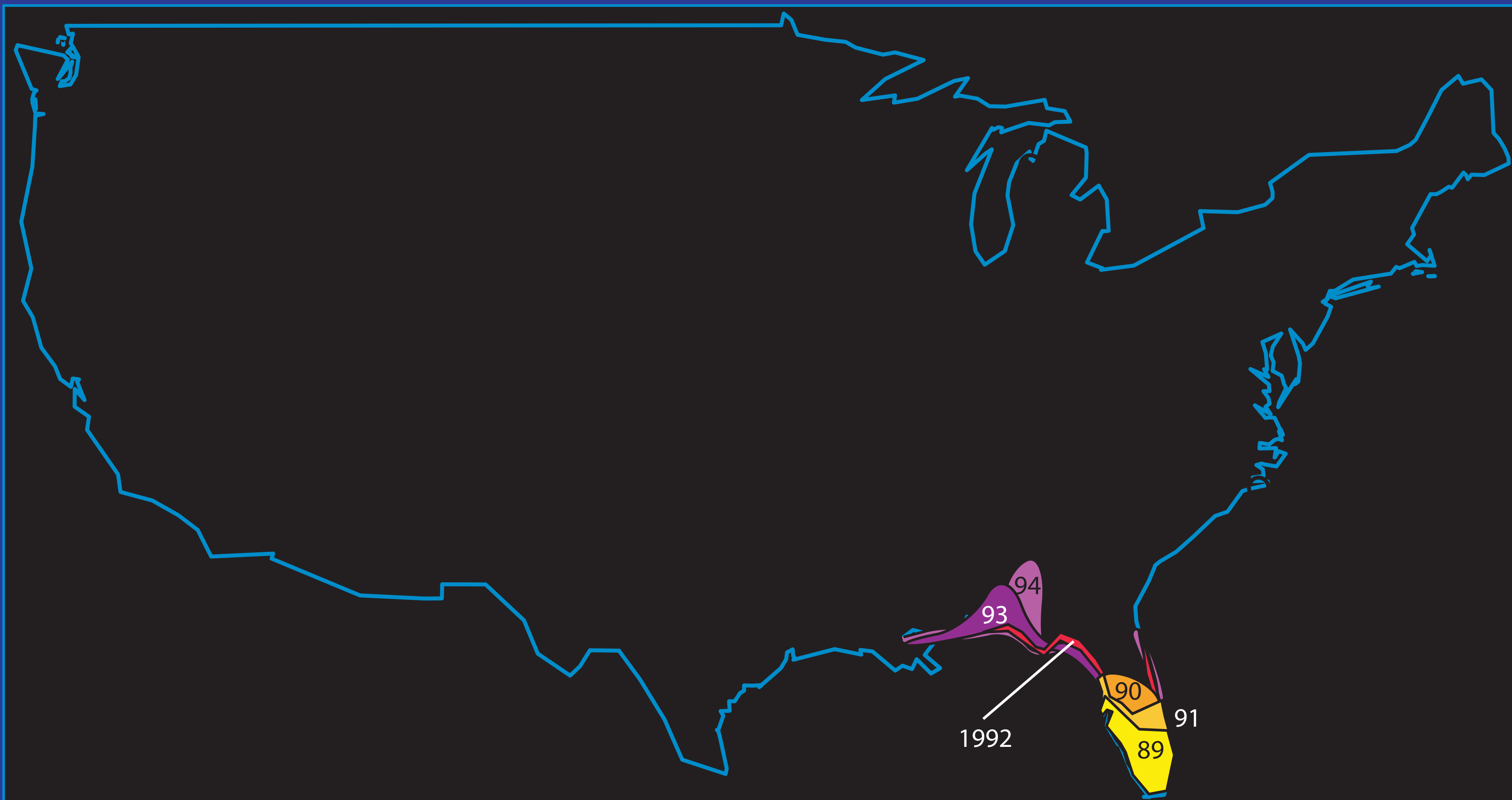


SOURCE: Audubon Christmas Bird Count

Winter Distribution 1989–2004

1994



SOURCE: Audubon Christmas Bird Count

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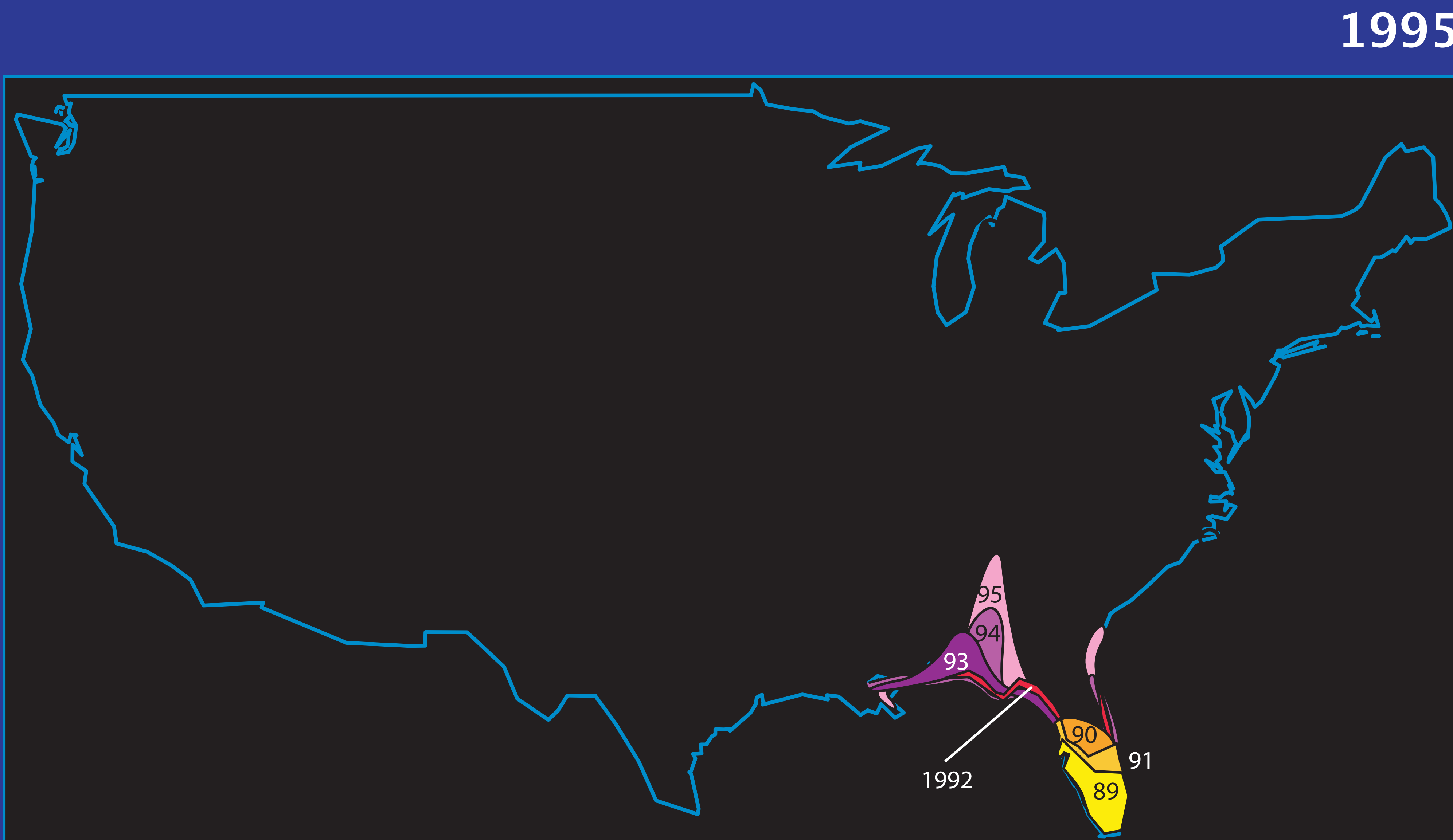

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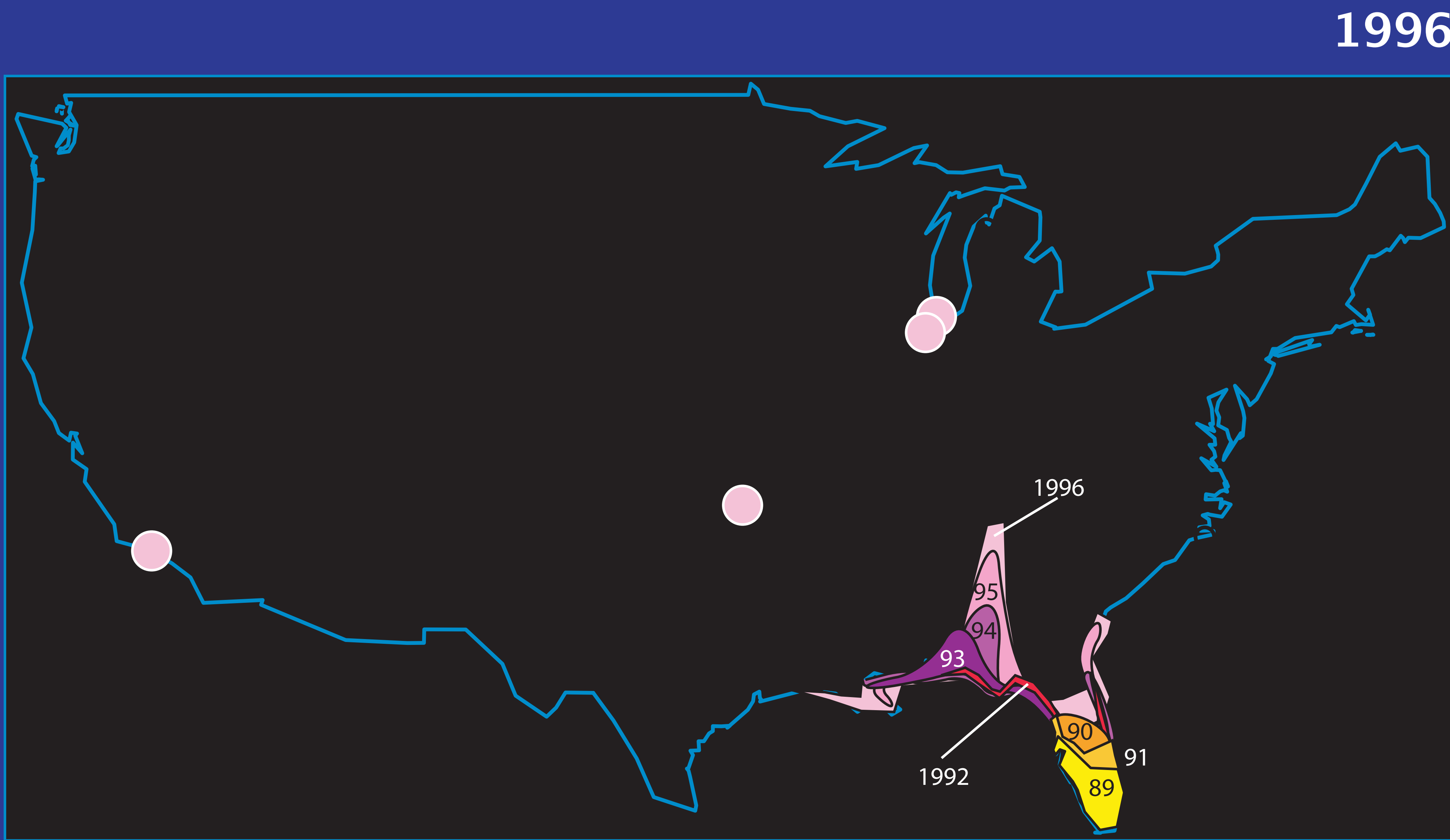
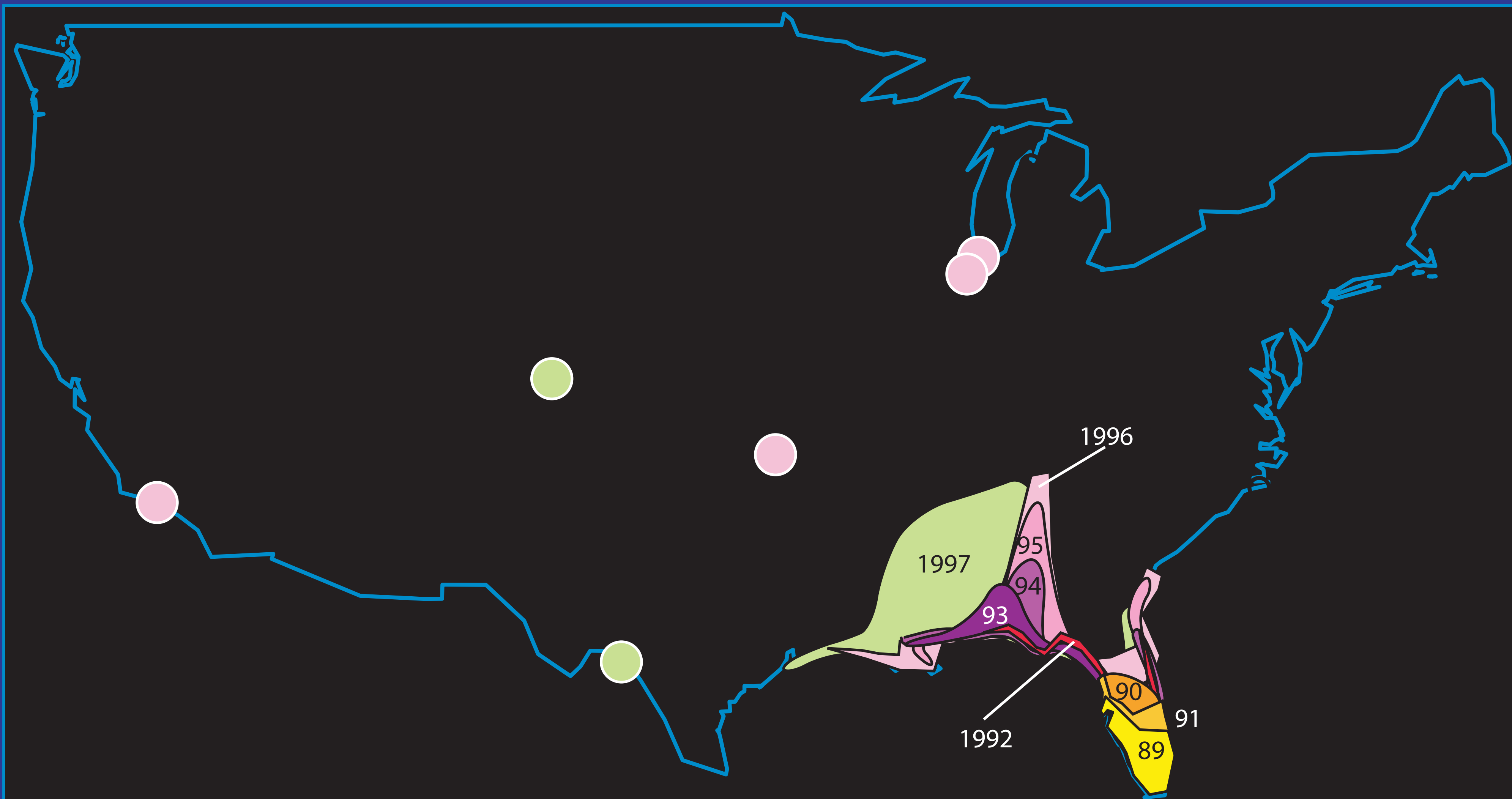


SOURCE: Audubon Christmas Bird Count

Winter Distribution 1989–2004

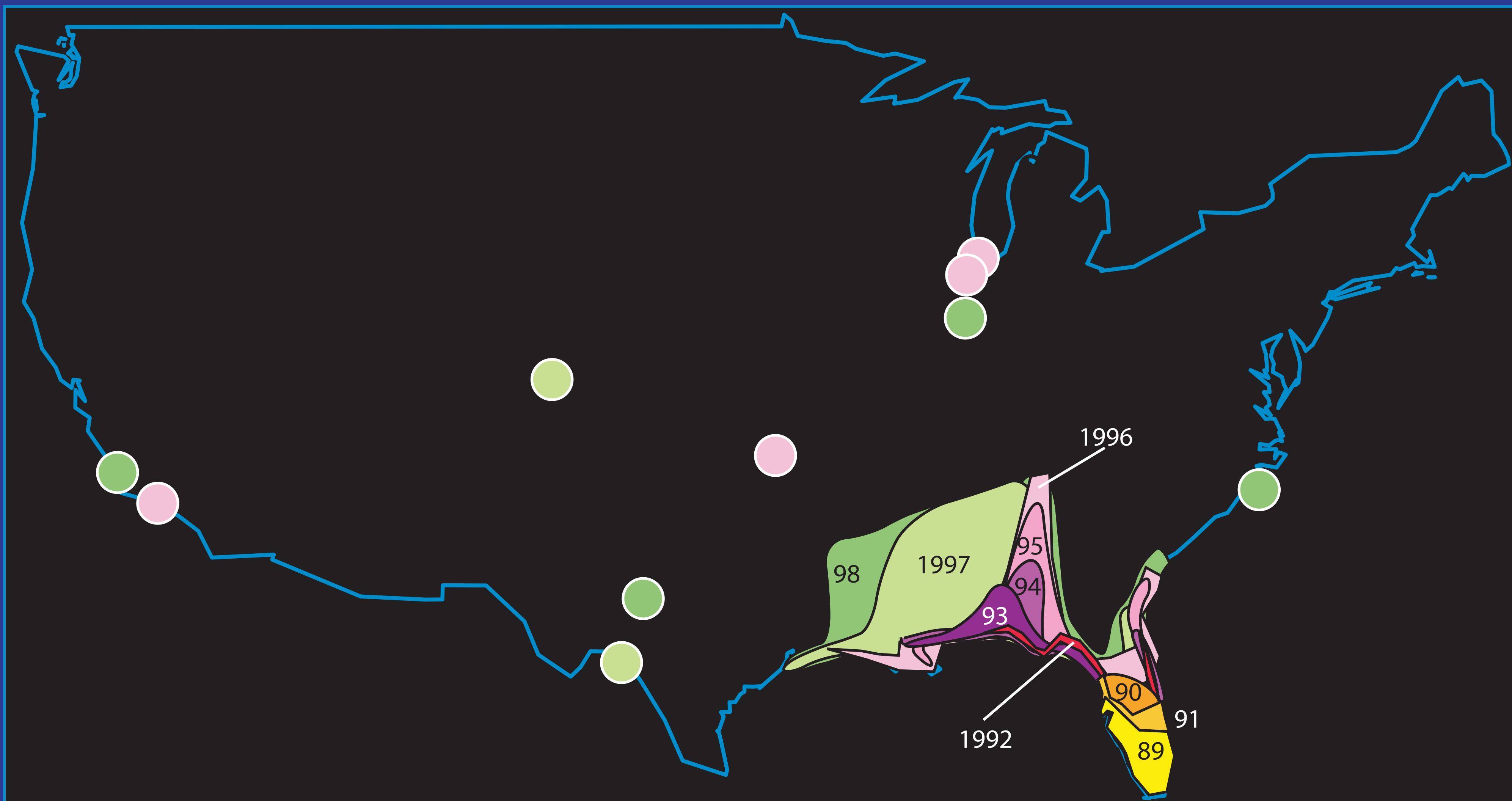
1997



SOURCE: Audubon Christmas Bird Count

Winter Distribution 1989–2004

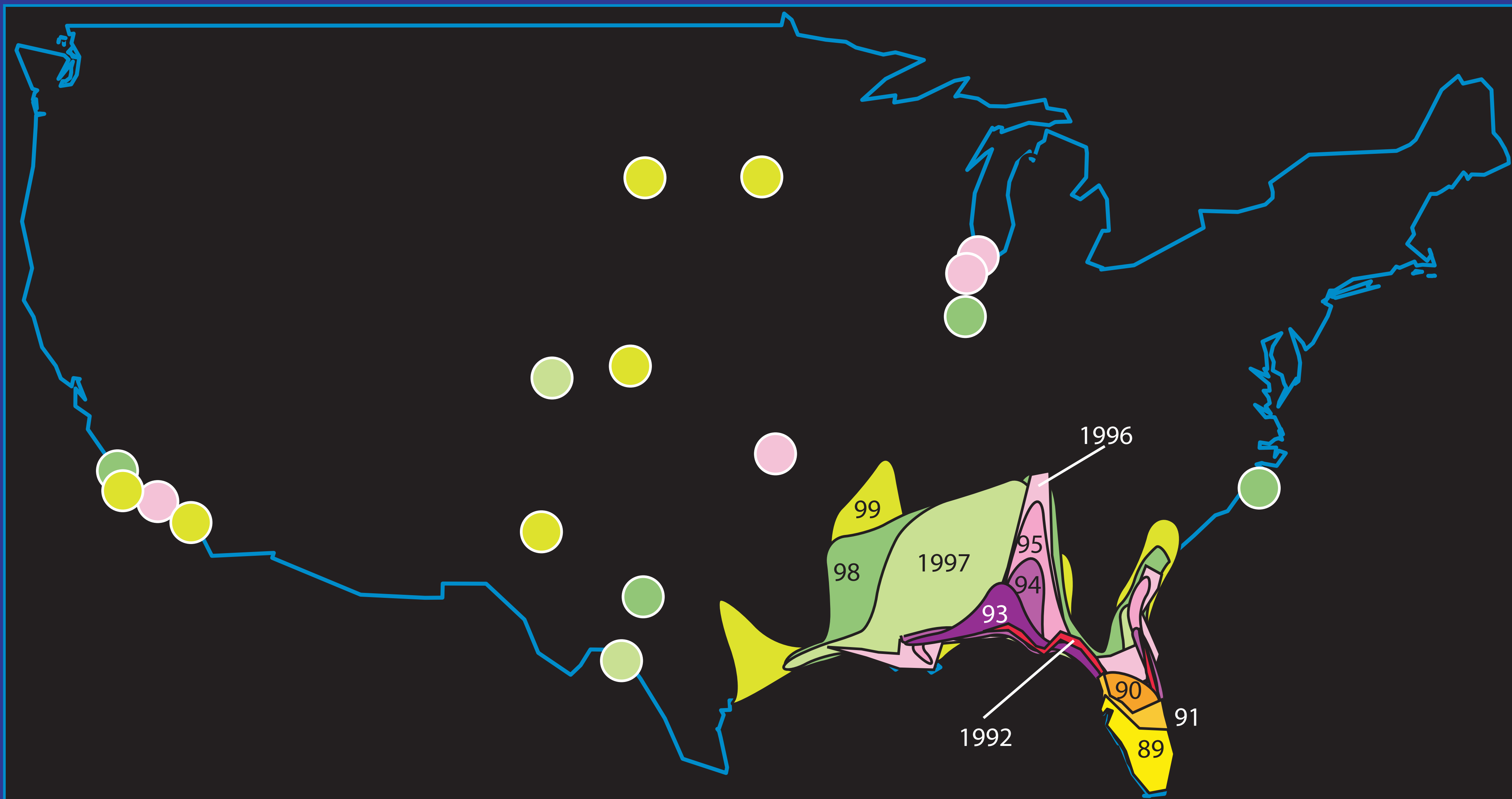
1998



SOURCE: Audubon Christmas Bird Count

Winter Distribution 1989–2004

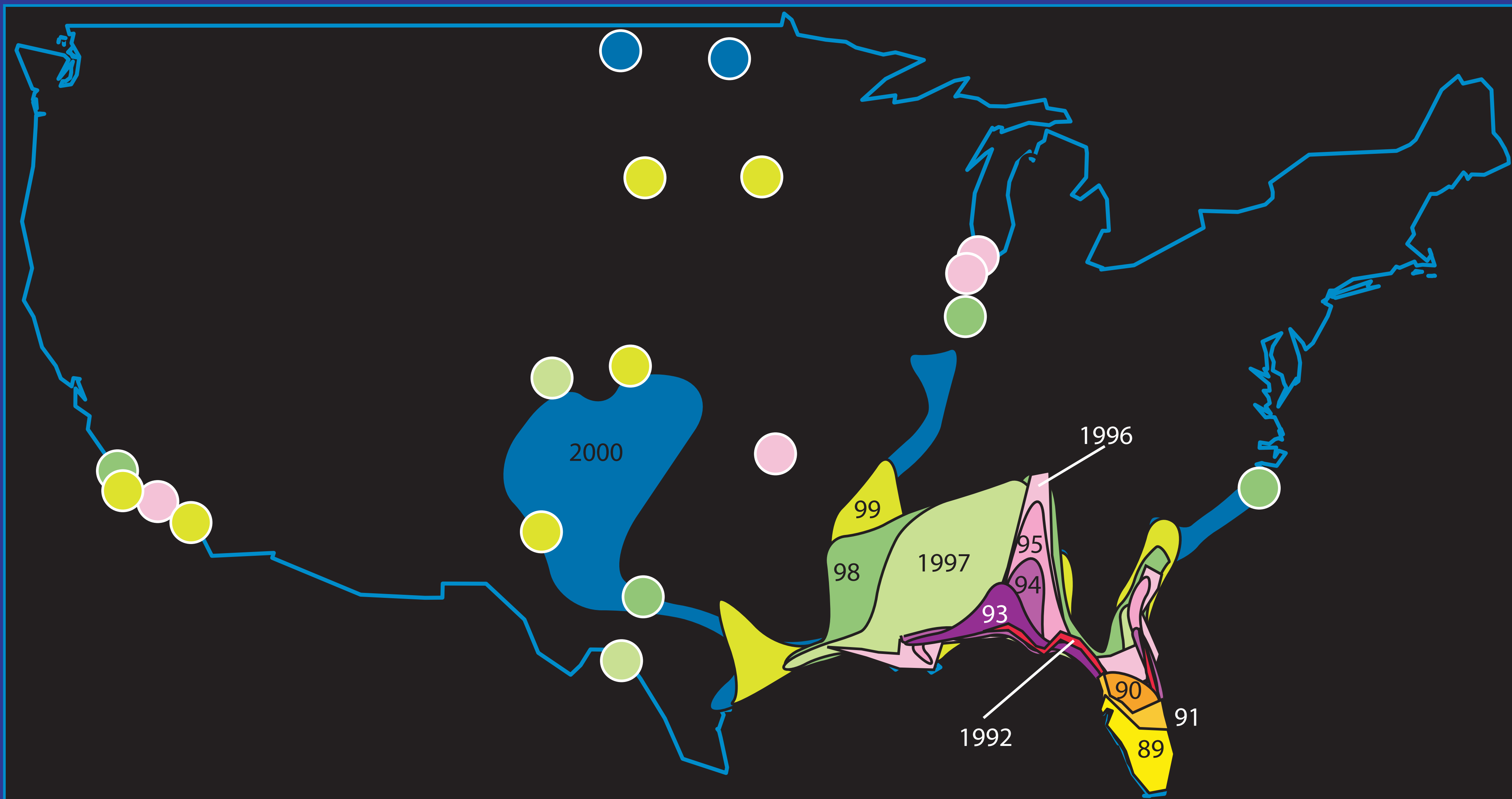
1999



SOURCE: Audubon Christmas Bird Count

Winter Distribution 1989–2004

2000



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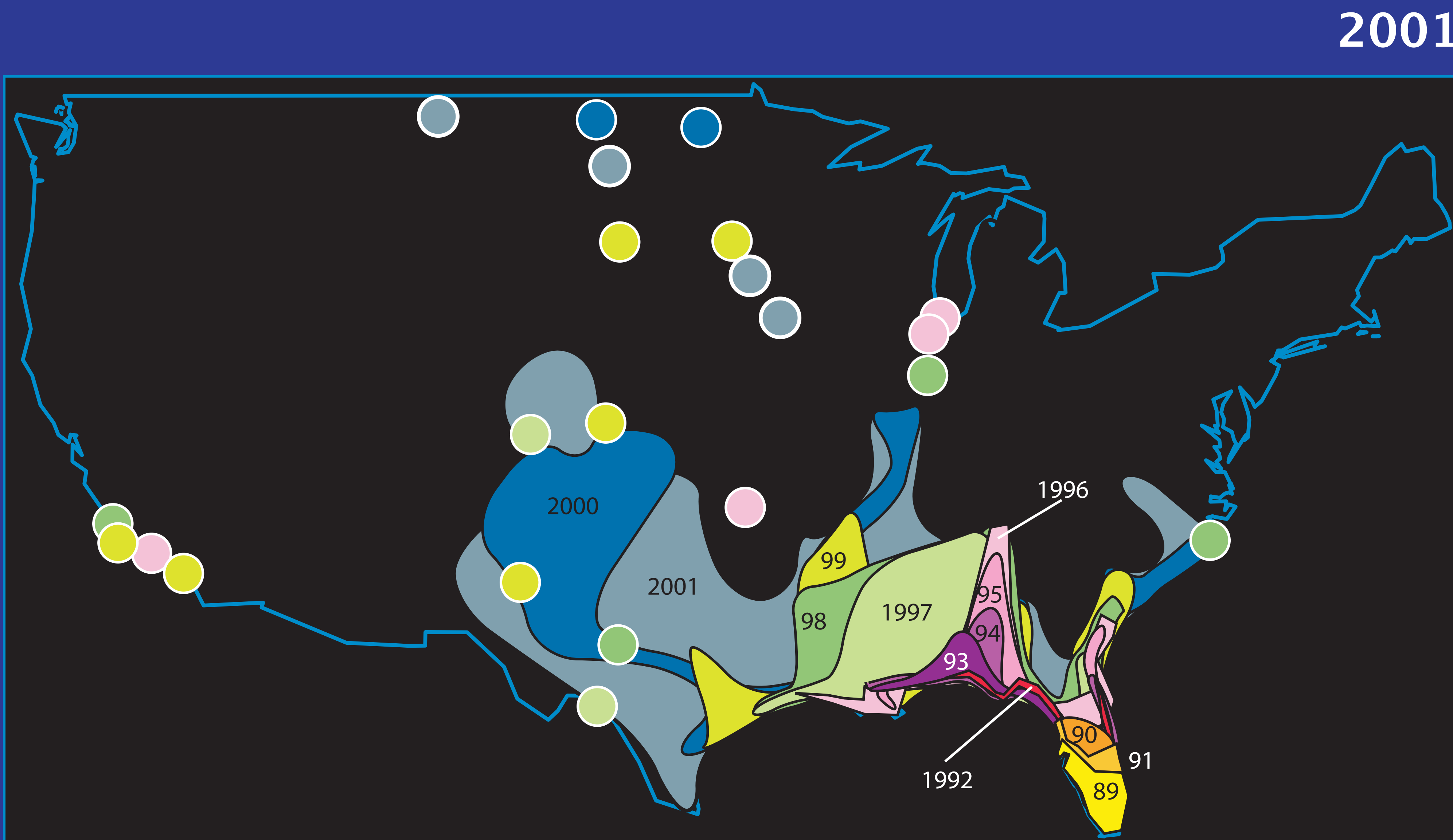
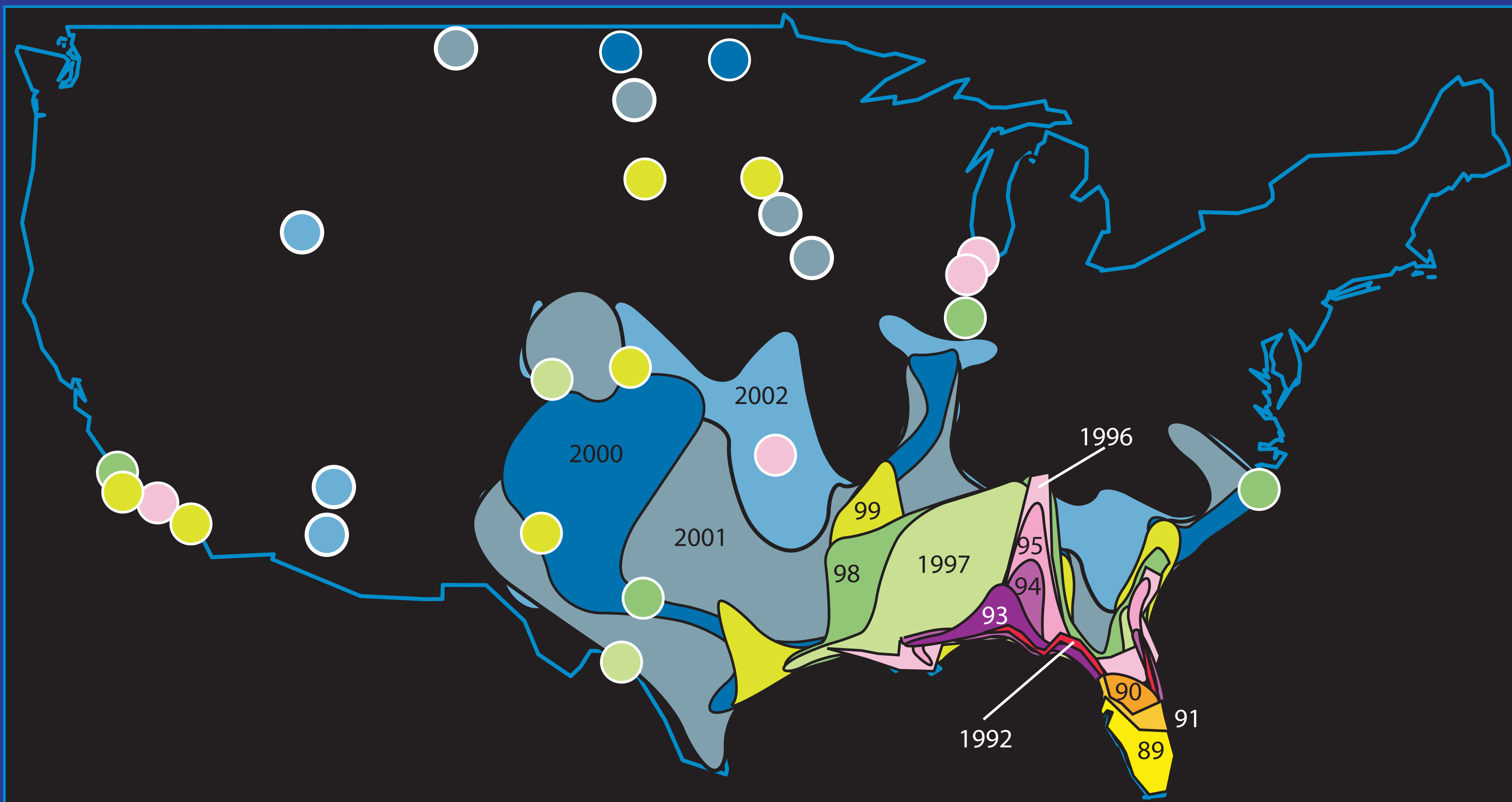
Winter Distribution 1989–2004



SOURCE: Audubon Christmas Bird Count

Winter Distribution 1989–2004

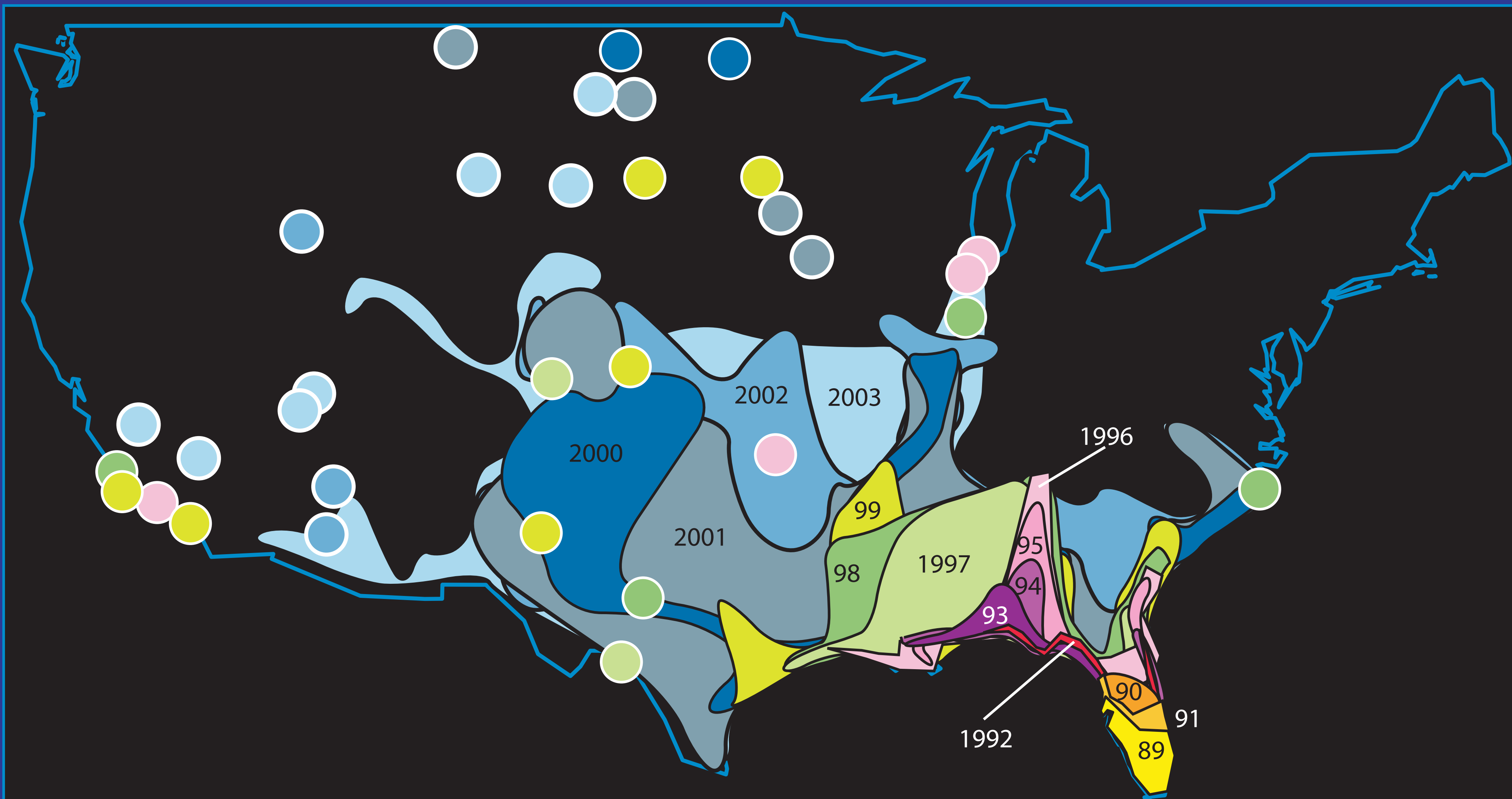
2002



SOURCE: Audubon Christmas Bird Count

Winter Distribution 1989–2004

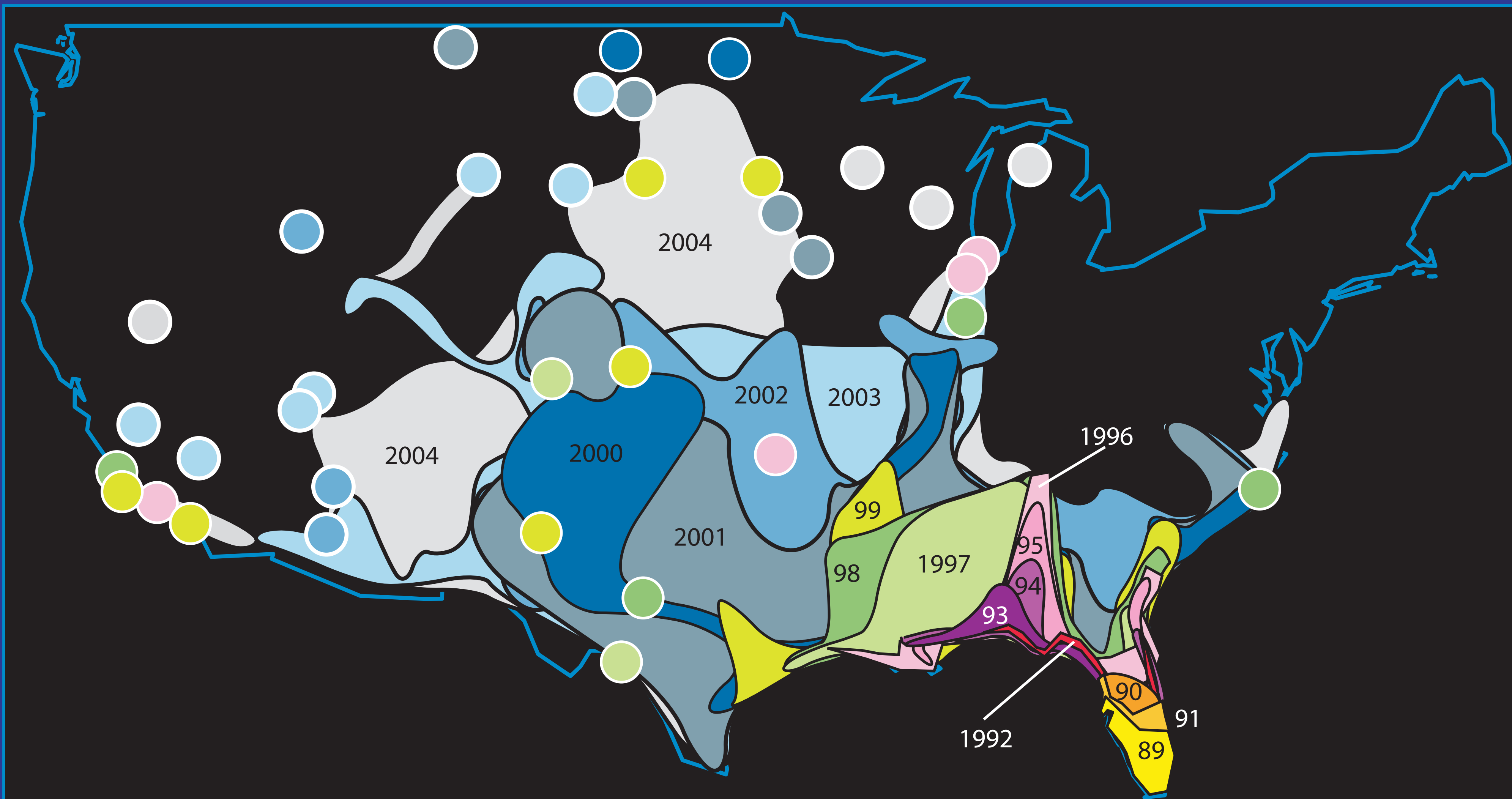
2003



SOURCE: Audubon Christmas Bird Count

Winter Distribution 1989–2004

2004



SOURCE: Audubon Christmas Bird Count

Invasion Dynamics of the Collared Dove

North American Invasion

- Introduced to Bahamas in 1970s
- Patchy distribution in Eastern US
- Long-distance dispersal events
- Multiple independent releases across the US
- Satellite populations in several western states and west coast

Spatially-Dependent-Breeding Model

Introducing spatial heterogeneity to the VL model

Spatial variation in length of breeding season

- Effects number of pairs, broods per pair, and local population density

Ecological Motivation

- Collared-dove is multi-brooded (up to 6 clutches per season)
- Number of broods constrained by length of growing season
- Growing season decreases with increasing latitude and elevation
- *Population densities should be lower at higher latitudes and elevation*

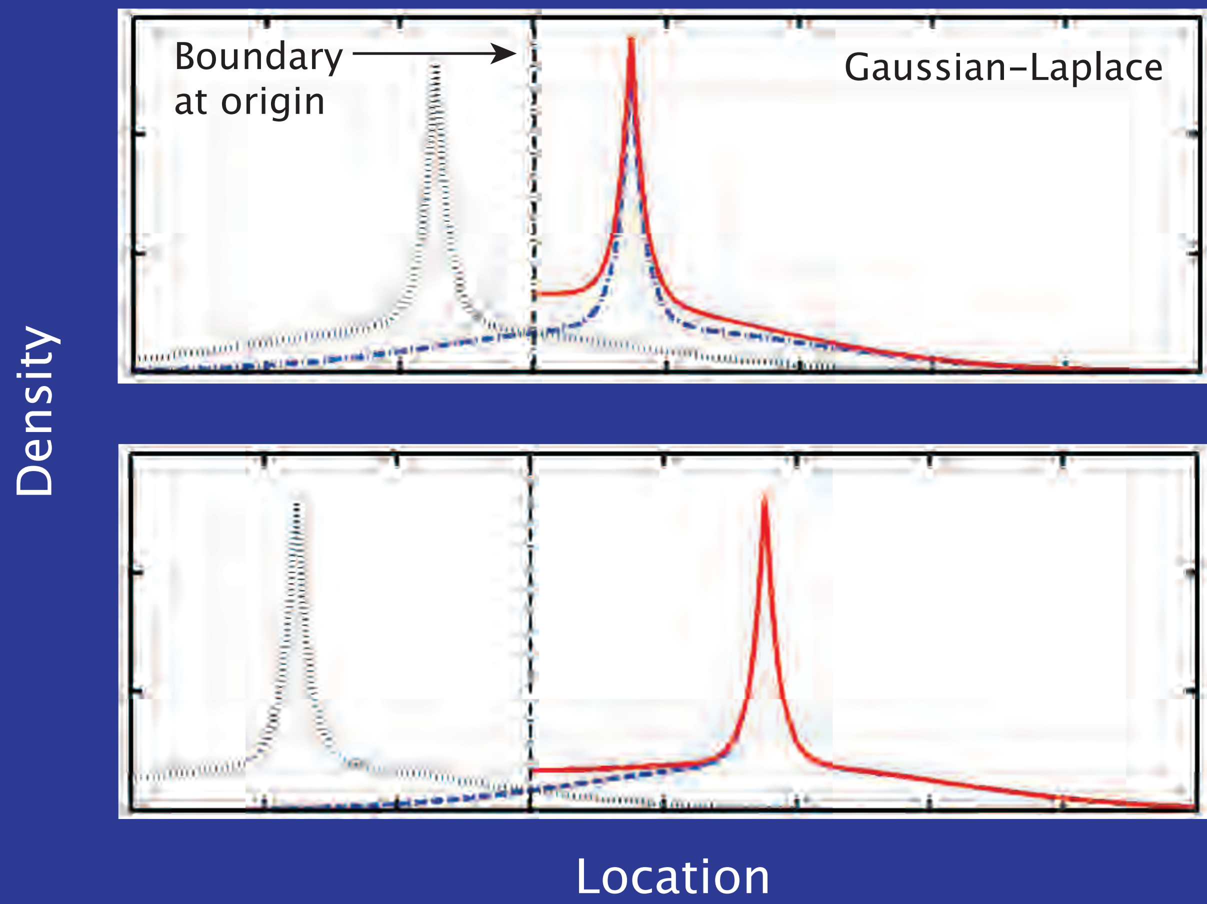
Estimating Growing Season Length

- 30-year average, number of frost-free days (Low Temp > 0° C)
- National Climate Data Center weather station database

Spatially-Dependent-Breeding Model

Dispersal Kernel

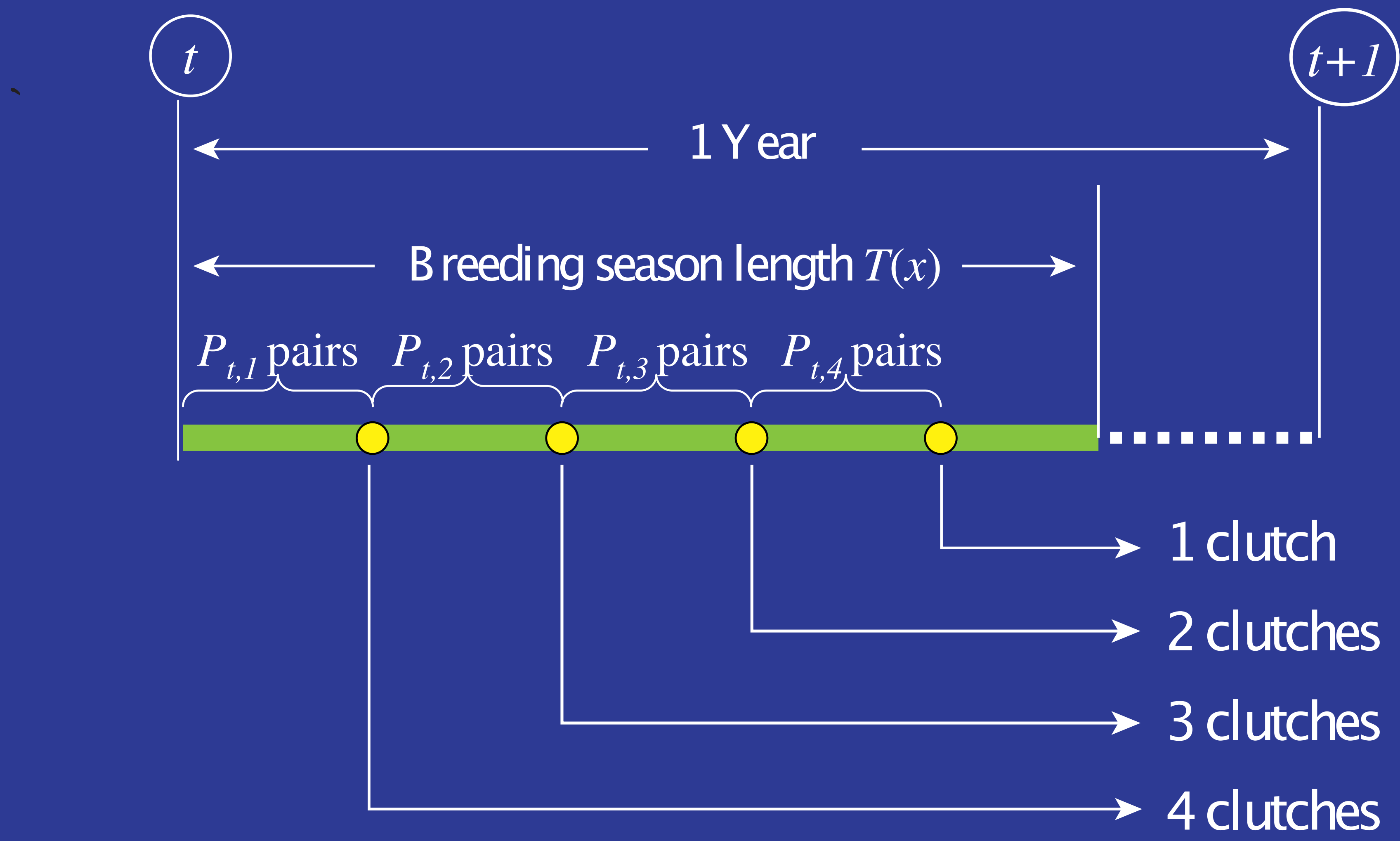
Reflective Boundary at Atlantic Ocean and Gulf of Mexico



Increased density along coasts and near origin of population

Variable Length Breeding Season

Effect of *T(x)* on pairs, broods, and local density

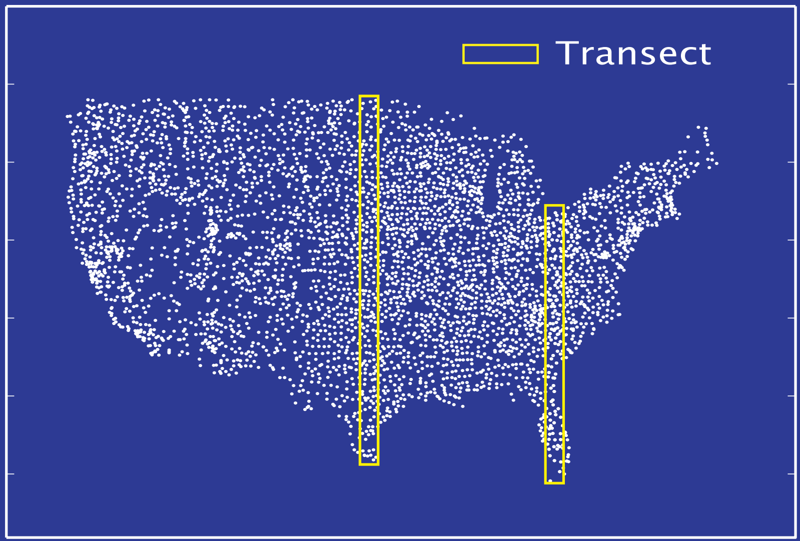


- Number of pairs formed increases over length of season
- Late season pairs produce fewer than max broods

Estimating Growing Season Length

- 30-year Average Frost-Free Days
- 2 North-South Linear Transects
- fit curves to estimate GSL along transect
- transects differ in topographic relief
- curve fits differ in residual variation

Locations of Weather Stations in NCDC Database



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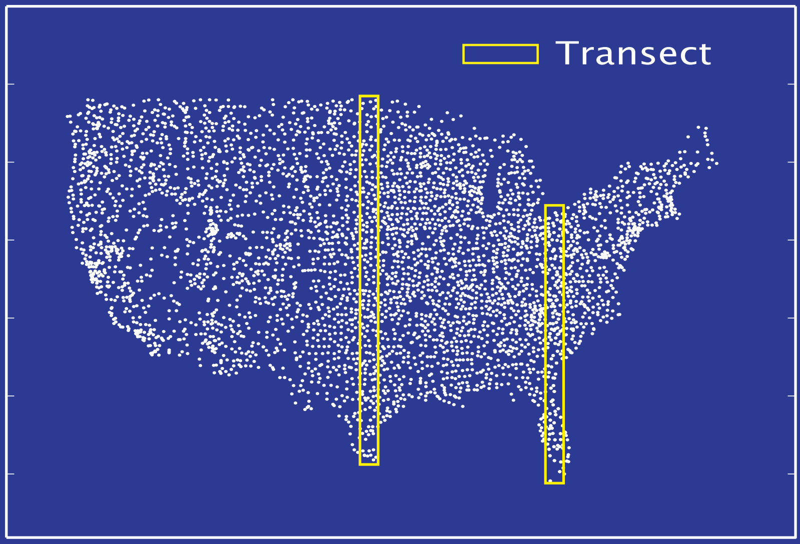
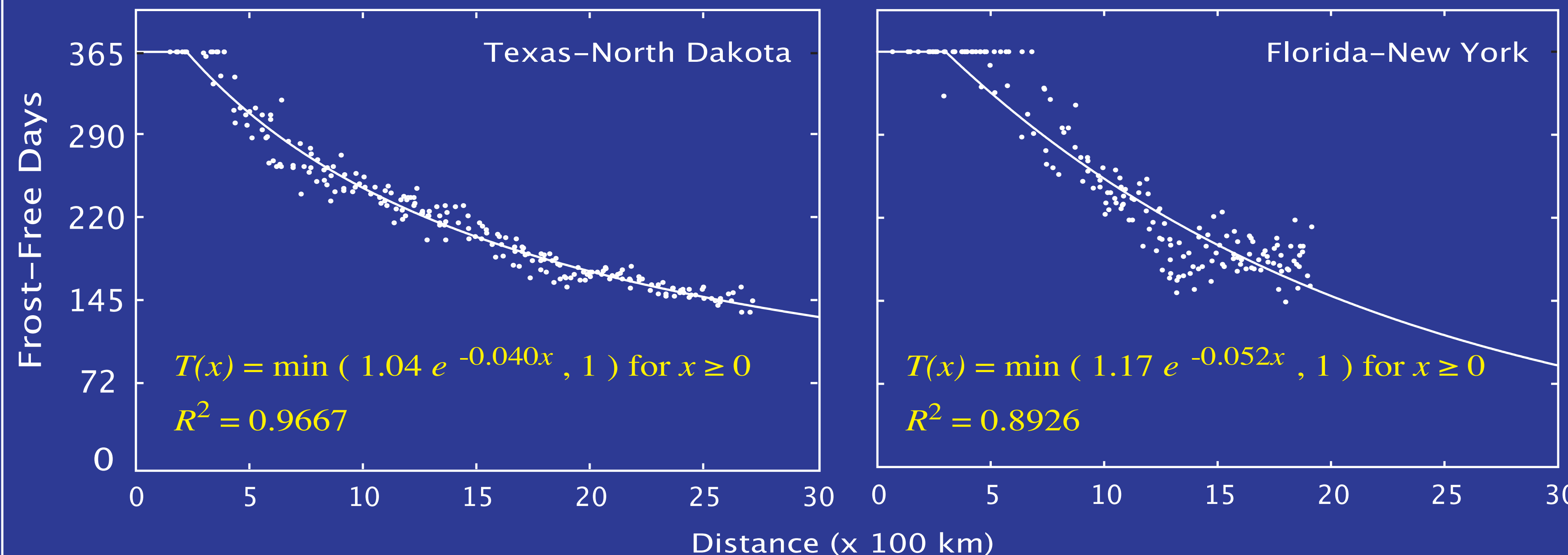


Variation in Frost-Free Days Along Transects



New Growth Function

Accounting for Spatio-Temporal Variation in Pairs, Nest Sites, and Offspring

Density unmated adults at x in i	$N_{t,i+1}(x) = N_{t,i}(x) - 2P_{t,i}(x)$
Density potential breeders at x in i	$P_{t,i+1}(x) = P[N_{t,i+1}(x)]$
Density actual breeders at x in i	$Q_{t,i+1}(x) = H[P_{t,i+1}(x) + R_{t,i}(x)]$
Density pairs no nest at x in i	$R_{t,i+1}(x) = P_{t,i+1}(x) - Q_{t,i+1}(x) + R_{t,i}(x)$
Density available nests at x in i	$\delta_{t,i+1}(x) = \delta_{t,i}(x) - Q_{t,i}(x)$
Total fledglings produced at x in i	$F_{t,i+1}(x) = (k-i)cQ_{t,i+1}(x)$

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Density available nests at x in i	$\delta_{t,i+1}(x) = \delta_{t,i}(x) - Q_{t,i}(x)$
Total fledglings produced at x in i	$F_{t,i+1}(x) = (k-i)cQ_{t,i+1}(x)$

Total fledglings produced at x in season: $F_t(x) = \sum_{i=1}^{k} F_{t,i}(x)$

New spatially dependent growth function: $f(N_t(x)) = sN_t(x) + F_t(x)$

Population density depends on number of possible broods and length of growing season.

Model Parameters

Parameter	Meaning	Source	Value
clutch size	eggs per pair	Literature	2
s	survival rate	Literature	0.49
c	rate of offspring production	Ave. clutch size x mean fledging success rate	0.56
σ	per capita rate of pair formation	estimated from CBC invasion speed	0.19
δ	nest site density	Published accounts of breeding bird densities	1.5 nests/km2

Christmas Bird Count

24 hour survey during a 2-week period around Christmas

Circular census area = 452.4 km^2

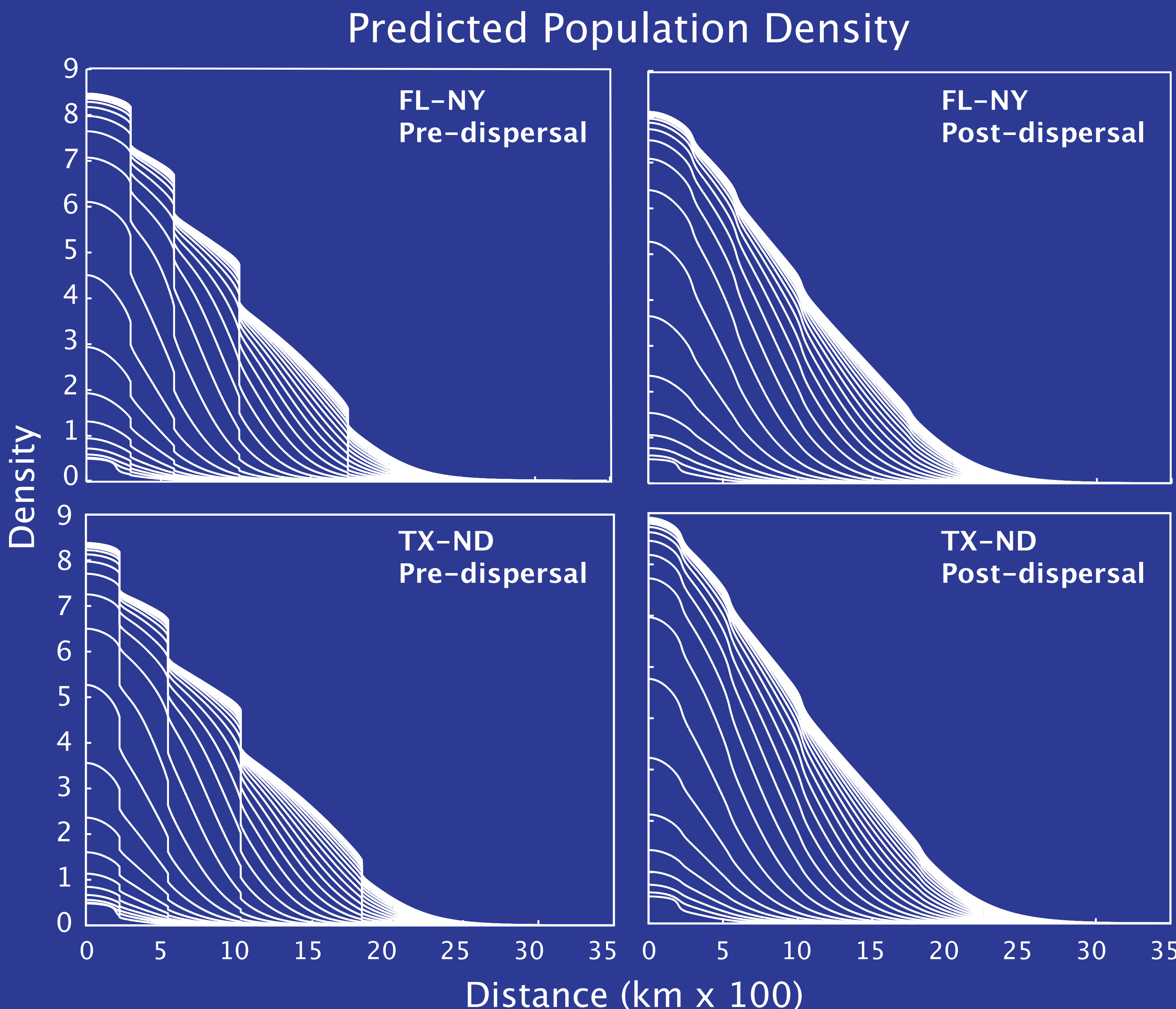
Testing the model: 1-dimension model

North American Breeding Bird Survey

3 minute survey, 50 stops, 0.8 km apart (road transect)

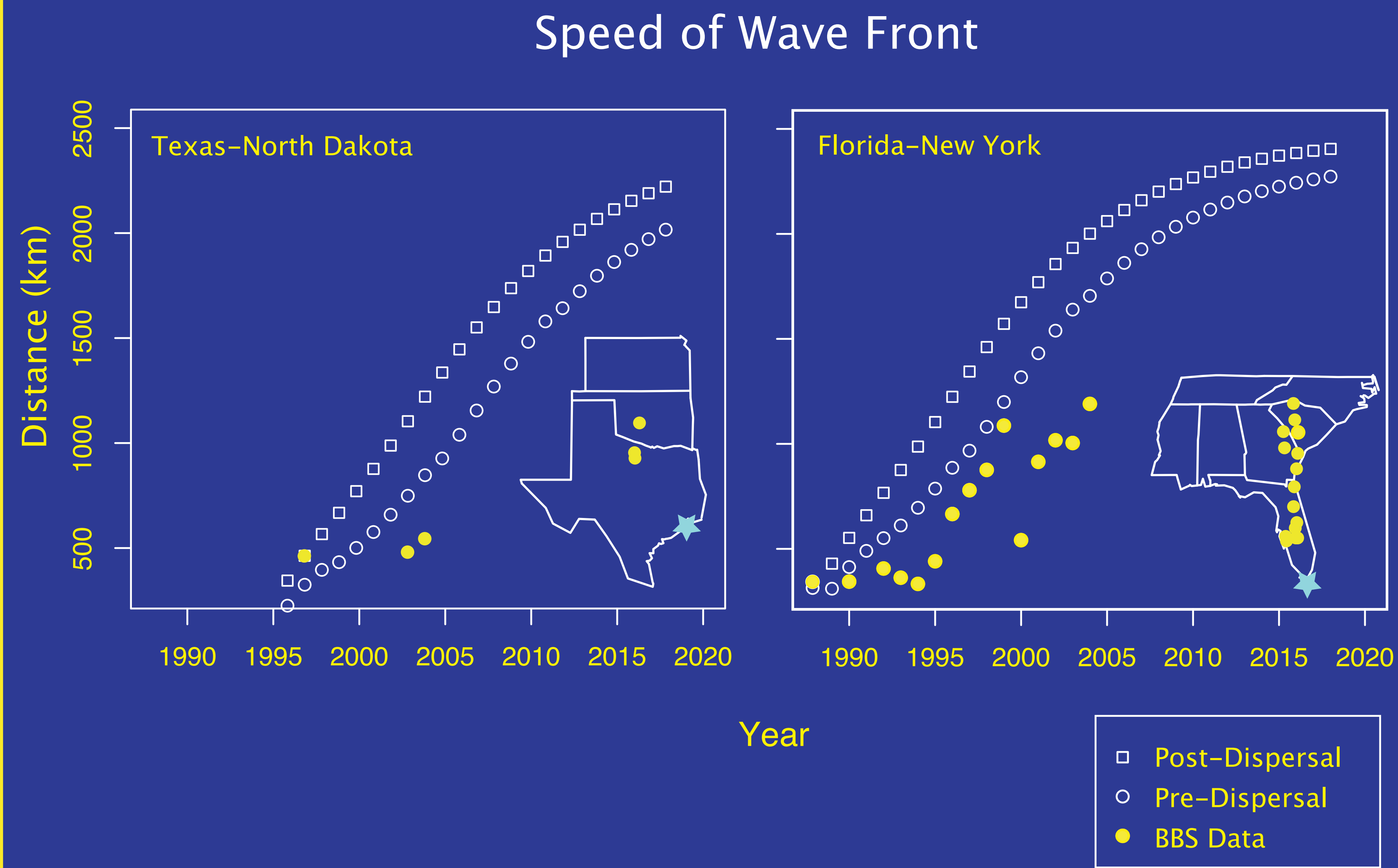
Linear transect = 39.4 km (approximately 32 km^2)

Results

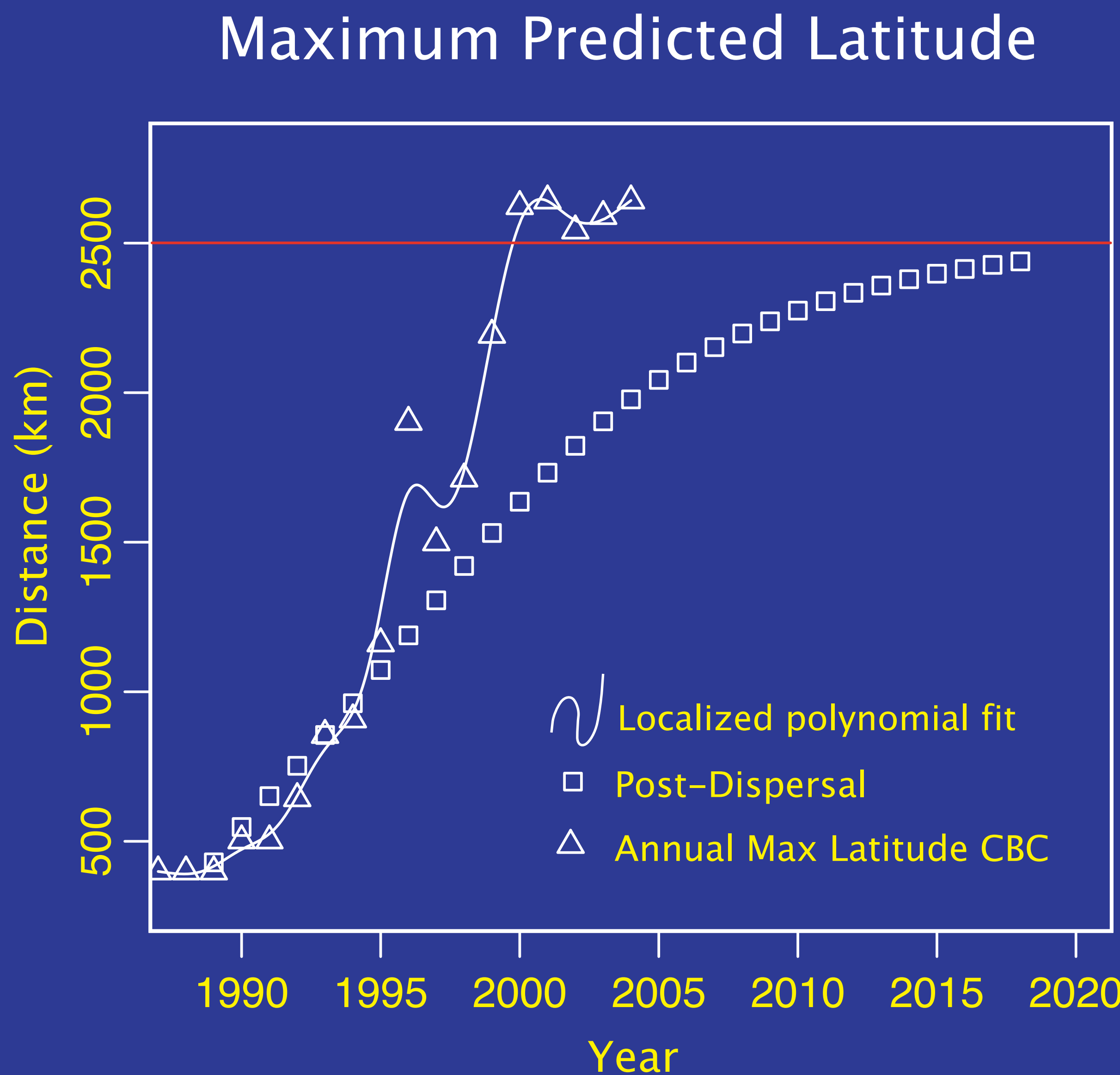


Predicted Population Density
FL–NY
Pre–dispersal
FL–NY
Post–dispersal
TX–ND
Pre–dispersal
TX–ND
Post–dispersal
Density
Distance (km x 100)
0
1
2
3
4
5
6
7
8
9
0
5
10
15
20
25
30
35

Results

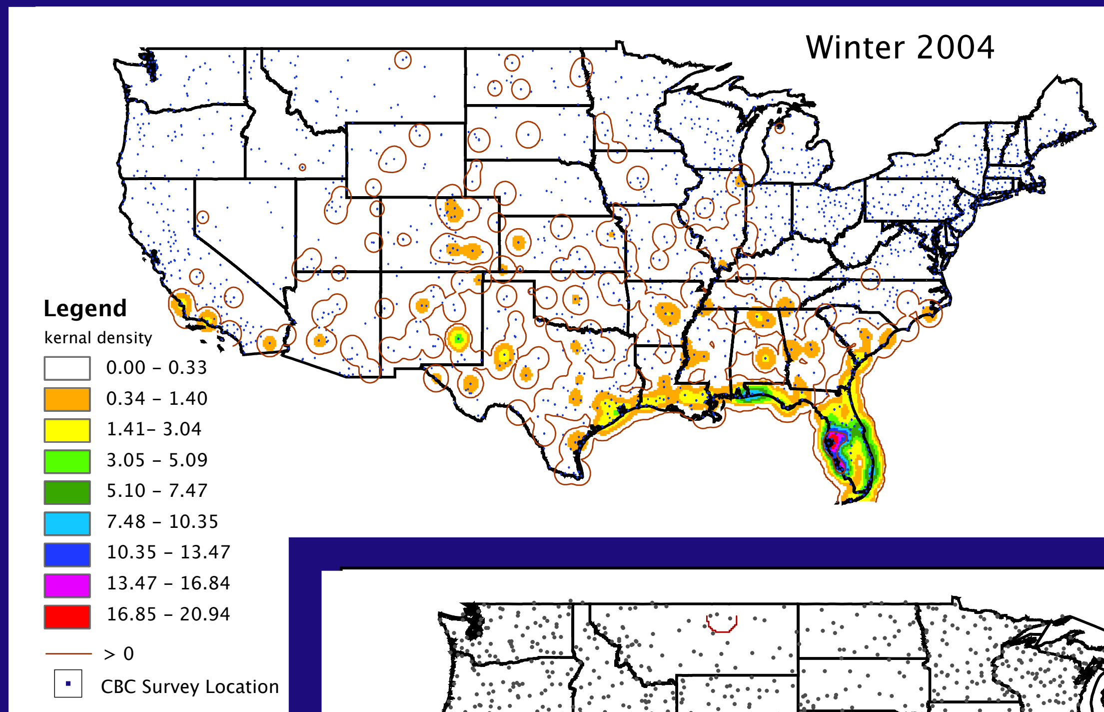

Speed of Wave Front
Distance (km)
Texas–North Dakota
Florida–New York
500
1000
1500
2000
2500
1990
1995
2000
2005
2010
2015
2020
Year
Post–Dispersal
Pre–Dispersal
BBS Data

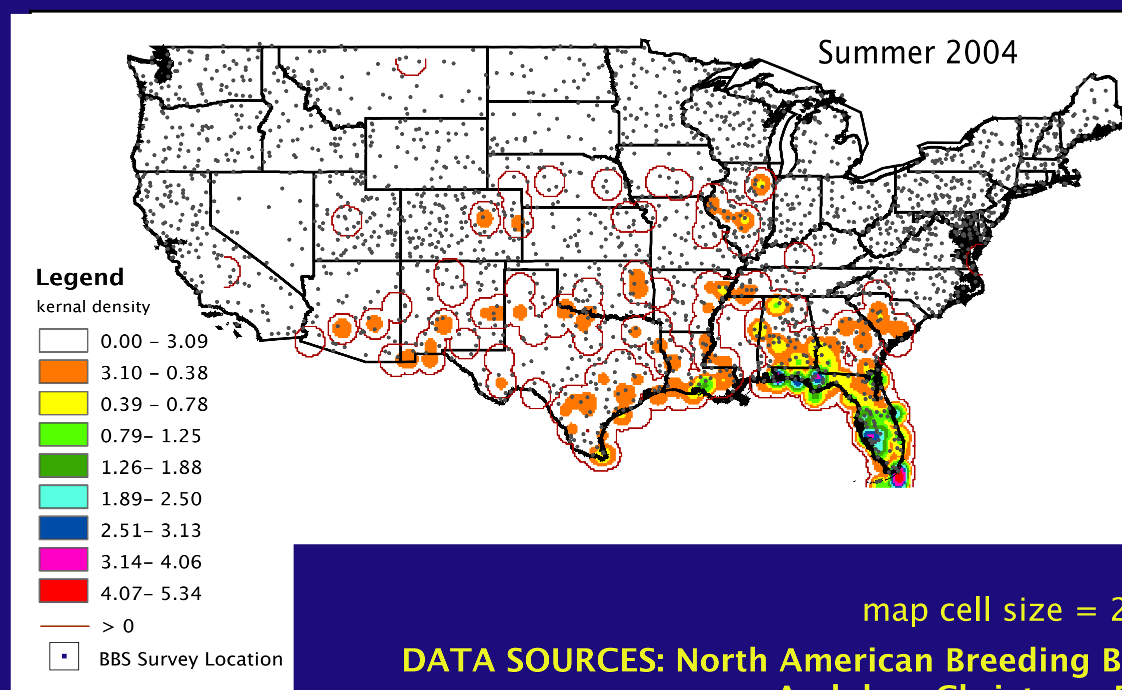
Results



Maximum Predicted Latitude
Distance (km)
500
1000
1500
2000
2500
1990
1995
2000
2005
2010
2015
2020
Year
Localized polynomial fit
Post-Dispersal
Annual Max Latitude CBC

Eurasian Collared-Dove Density (km^2)





map cell size = 20,000 km^2

DATA SOURCES: North American Breeding Bird Survey
Audubon Christmas Bird Count

Summary

APPROACH

- Integro-difference equation model
- Base-model = Veit-Lewis 2-stage model
- Spatially-dependent breeding model

PREDICTIONS

- Stepped wave shape (unverified empirically)
- Wave speed faster in East-West direction
- Higher population densities near coasts, great lakes
- Maximum latitude of range spread (approx. 50 degrees)
- Rate of invasion slower at higher latitudes and elevations

Conclusions & Future Work

Spatially-dependent-breeding model (IDE)

- Useful for multi-brooded species
- Adaptable to many spatial features (e.g. habitat type, NPP, etc)
- Macro-ecological spatial scales

Future Work

- 2-Dimensional analysis
- Multi-species models
- Competition (collared dove x mourning dove, others)

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Co-Authors

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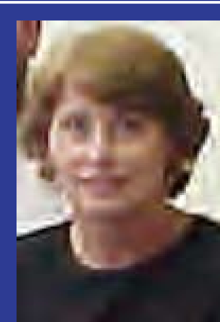

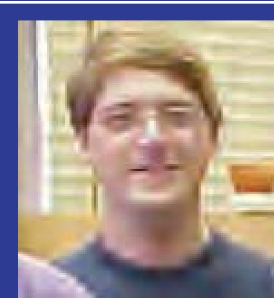

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