Models of Bird Migration

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Outline

- Flight Theory: how far can a bird fly with a given amount of fuel (fat)
- Using static optimization to find optimal migration schedules: when should a bird leave a stopover site?
- Optimal Migration schedules: use of state-variable models in migration

Theory of Flight (Simplest Version)

•increment in Flight distance with decrease in body mass due to fuel consumption is proportional to Lift:drag ratio and inversely proportional to body mass

$$\frac{dY}{dM} \propto \frac{L/D}{M}$$

•in an “ideal” bird L/D is proportional to 1/square root of mass

$$\frac{dY}{dM} \propto \frac{1}{M^{\frac{3}{2}}}$$

•gives the simplest Range Equation. f is fuel load (g of fat/lean body mass)

$$Y = c\left(1 - \frac{1}{\sqrt{(1+f)}}\right)$$

Theory of Flight

- Simplest range equation $Y = c(1 - \frac{1}{\sqrt{(1+f)}})$
- There are many others
- All theory is based on Fixed wing aircraft aerodynamics
- Pennycuick's FLIGHT program simulates flight and fuel consumption in ten minute increments

FLIGHT program

Simulates fuel usage and muscle burning in ten minute increments throughout a migratory flight

Can be downloaded from Colin Pennycuick's homepage at University of Bristol, Biological Sciences

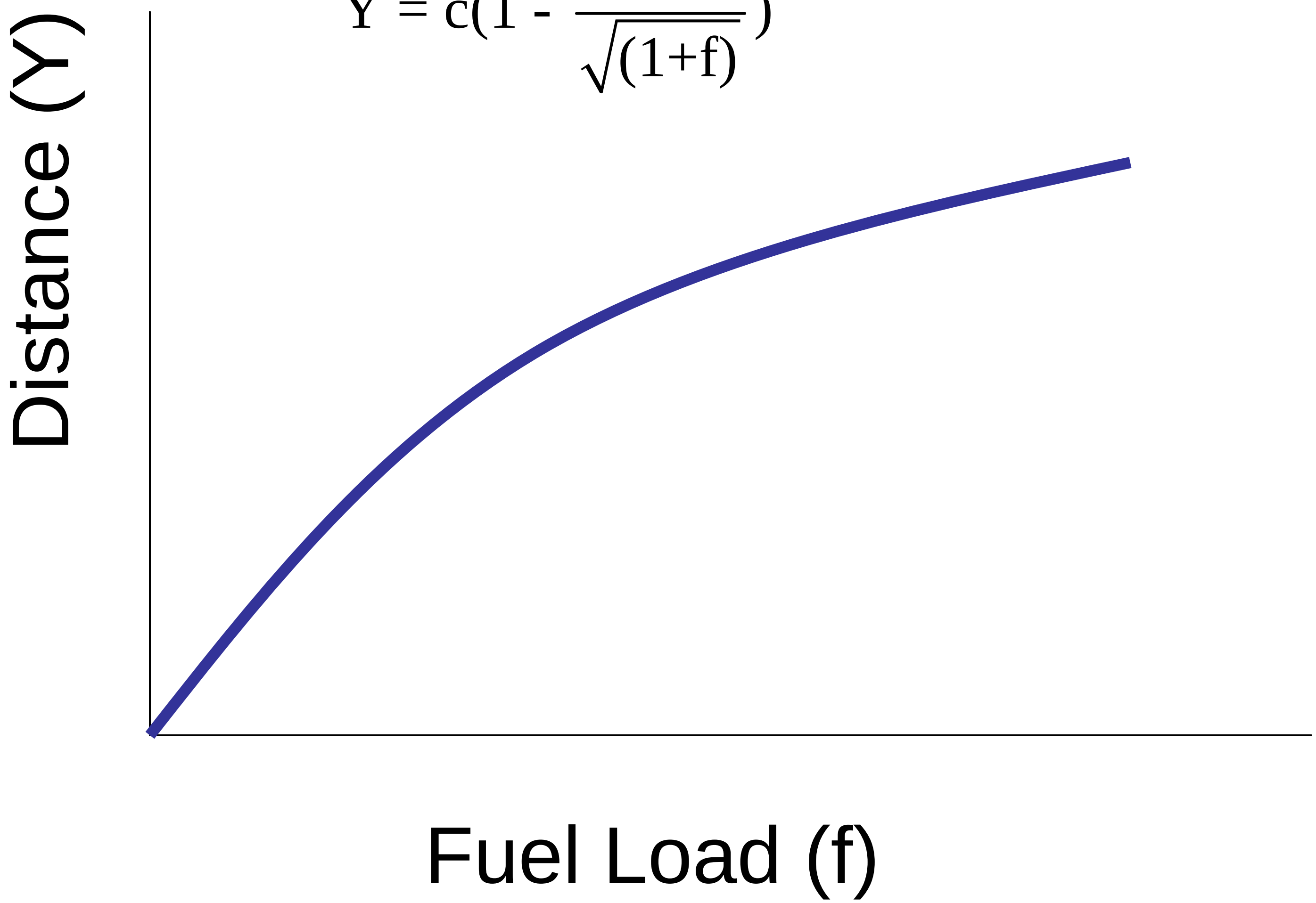
http://www.bio.bris.ac.uk/people/staff.cfm?key=95

or search on "Penncuick FLIGHT"

Jeff Kelly's netlogo tool :
http://www.migrate.ou.edu/netlogo/pennycuick-1.nlogo.html

Range Equation

$$Y = c\left(1 - \frac{1}{\sqrt{(1+f)}}\right)$$



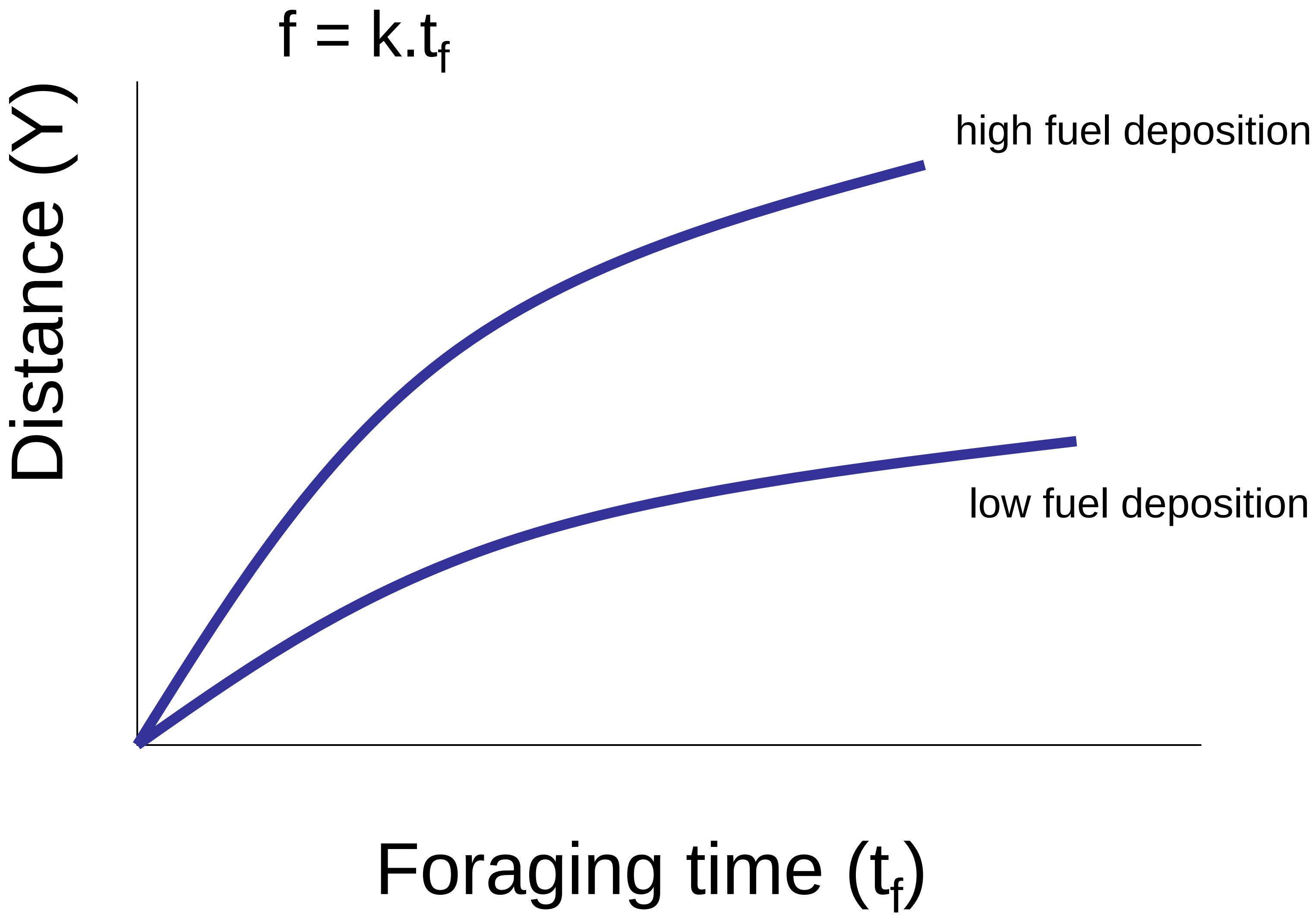
Optimal migration schedules

- Evolution by means of natural selection is a process of optimization
- individuals are behaving so as to maximize their fitness
- components of fitness: number of offspring, quality of offspring, *survival*
- for finding optimal migration strategies, we need a surrogate currency

During migration, what is a bird doing to maximize fitness?

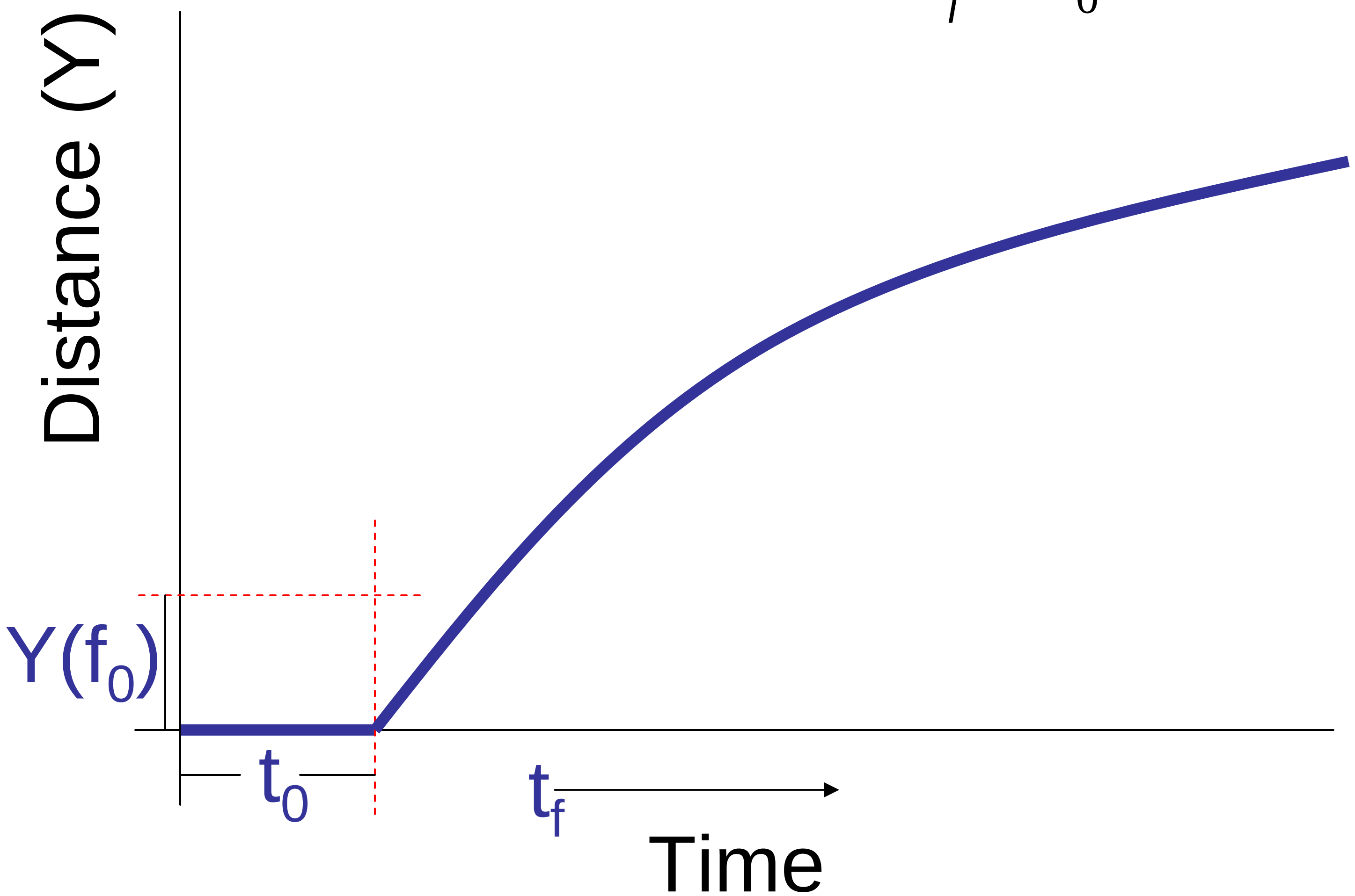
- Minimize *TIME*: maximize overall speed of migration
- Minimize *PREDATION*
- Minimize *ENERGY*, if food is scarce during migration
- Combination of *currencies*

Range Equation in units of foraging time



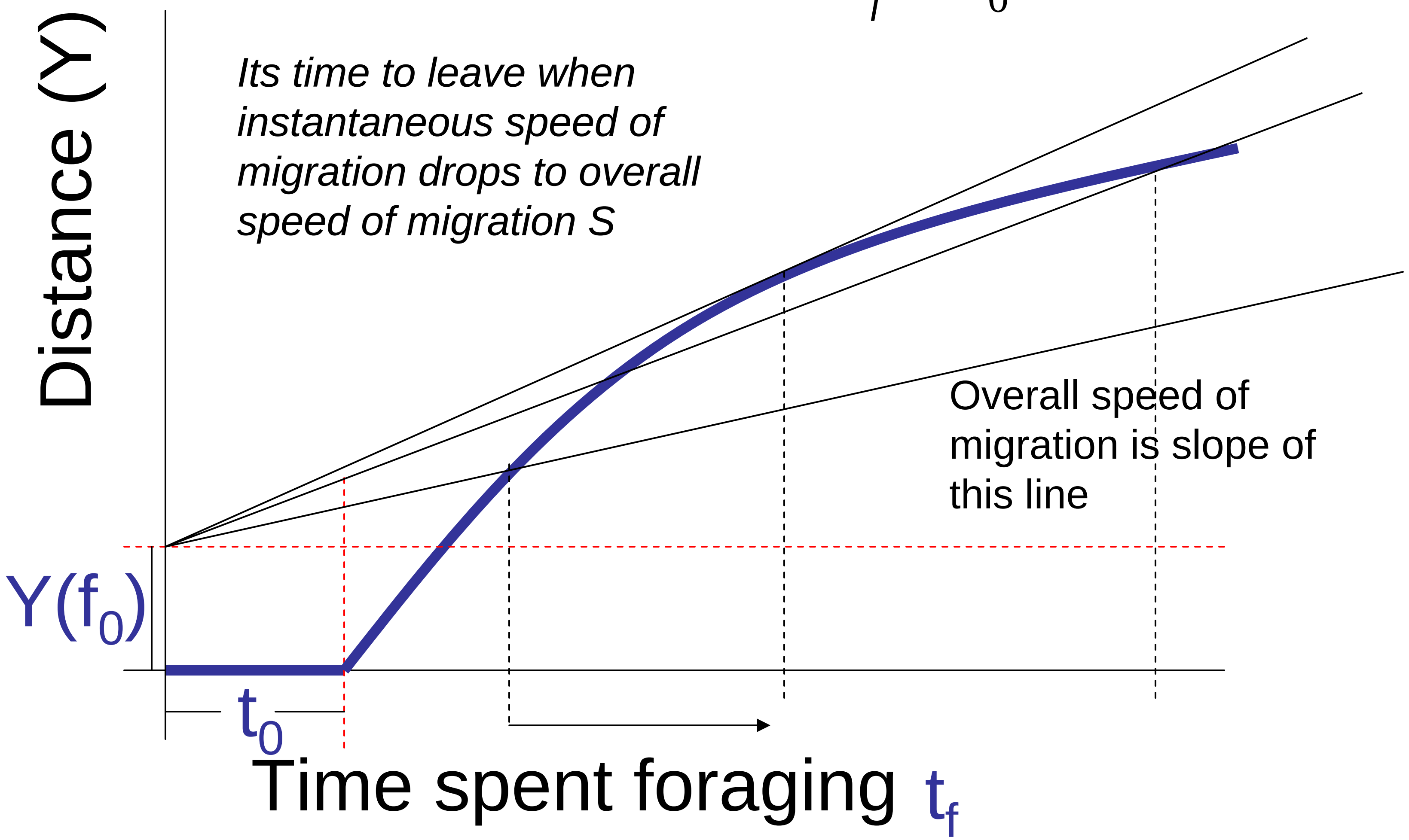
Minimize Time

maximize overall speed migration: $$\frac{Y - Y(f_0)}{t_f + t_0}$$

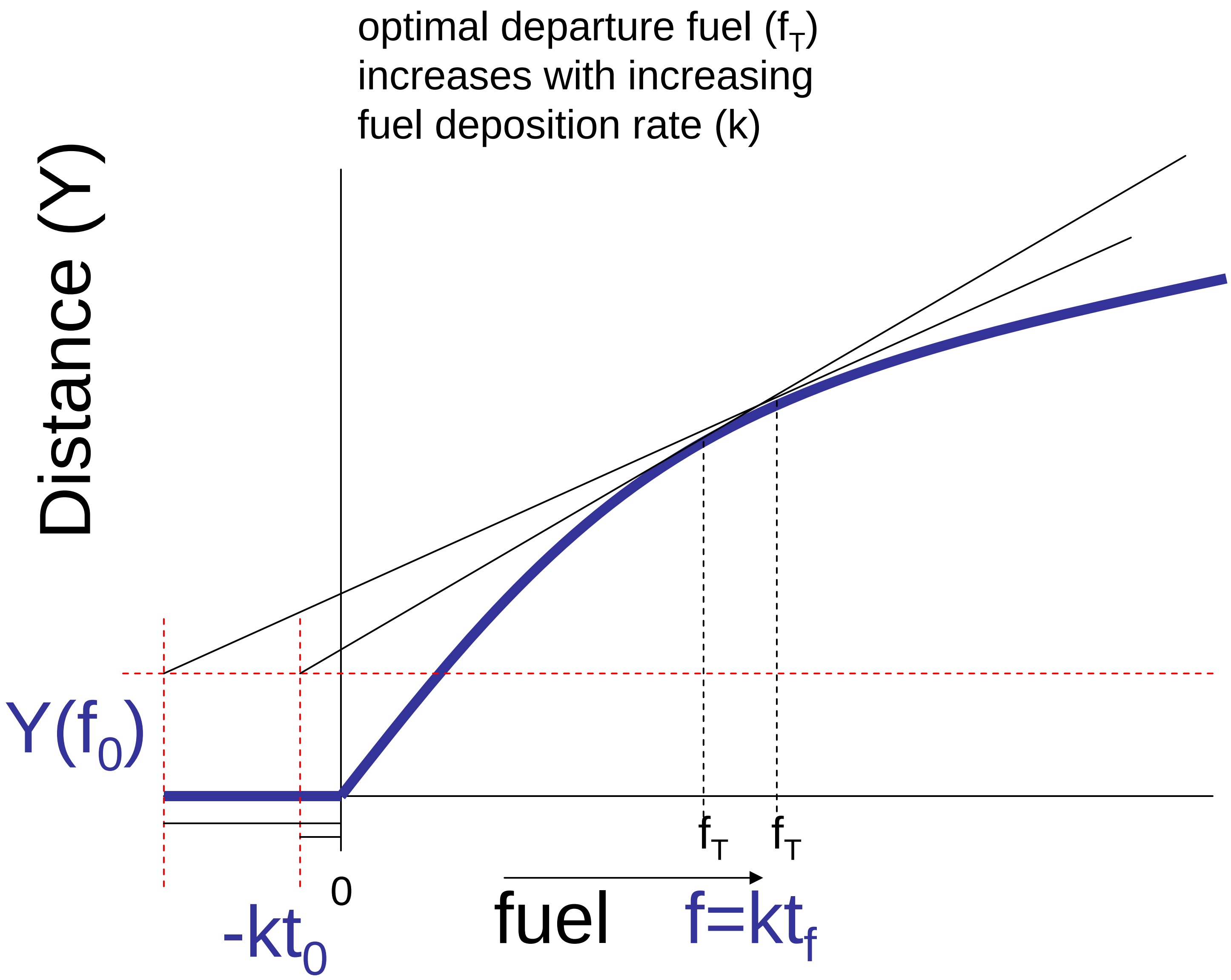


Minimize Time

maximize overall speed migration: $$\frac{Y - Y(f_0)}{t_f + t_0}$$

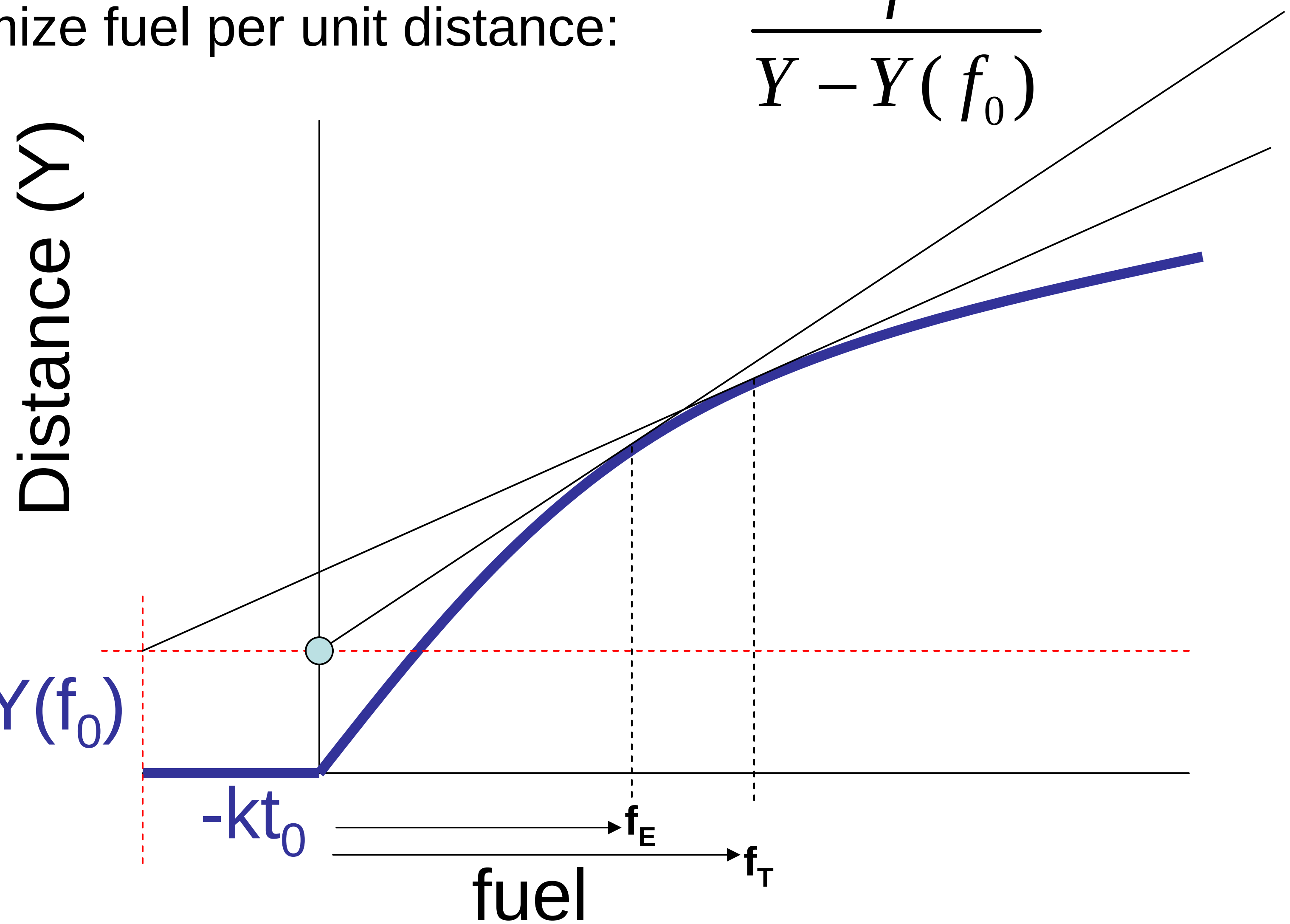


Minimize Time

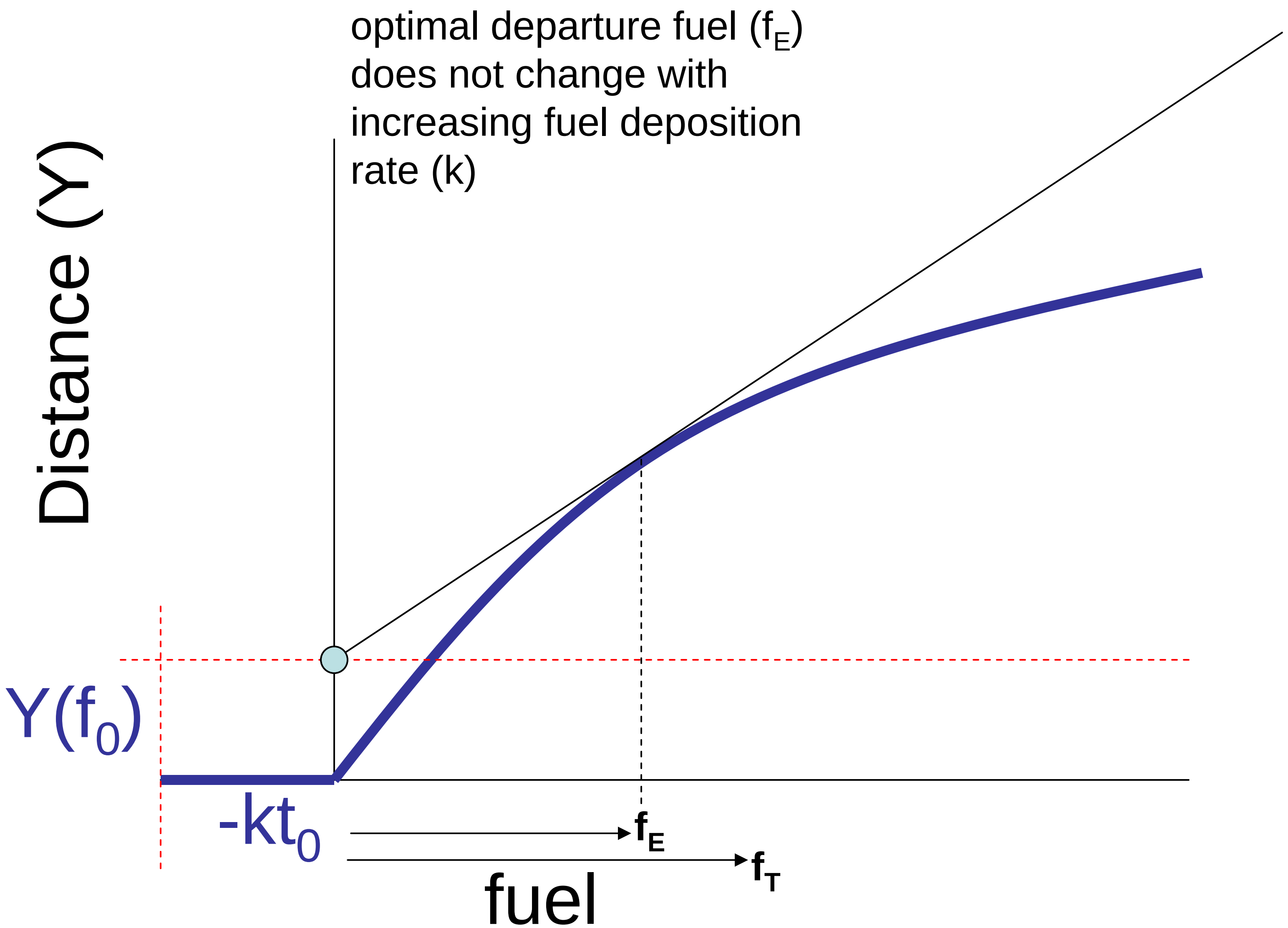


Minimize energy cost of transport

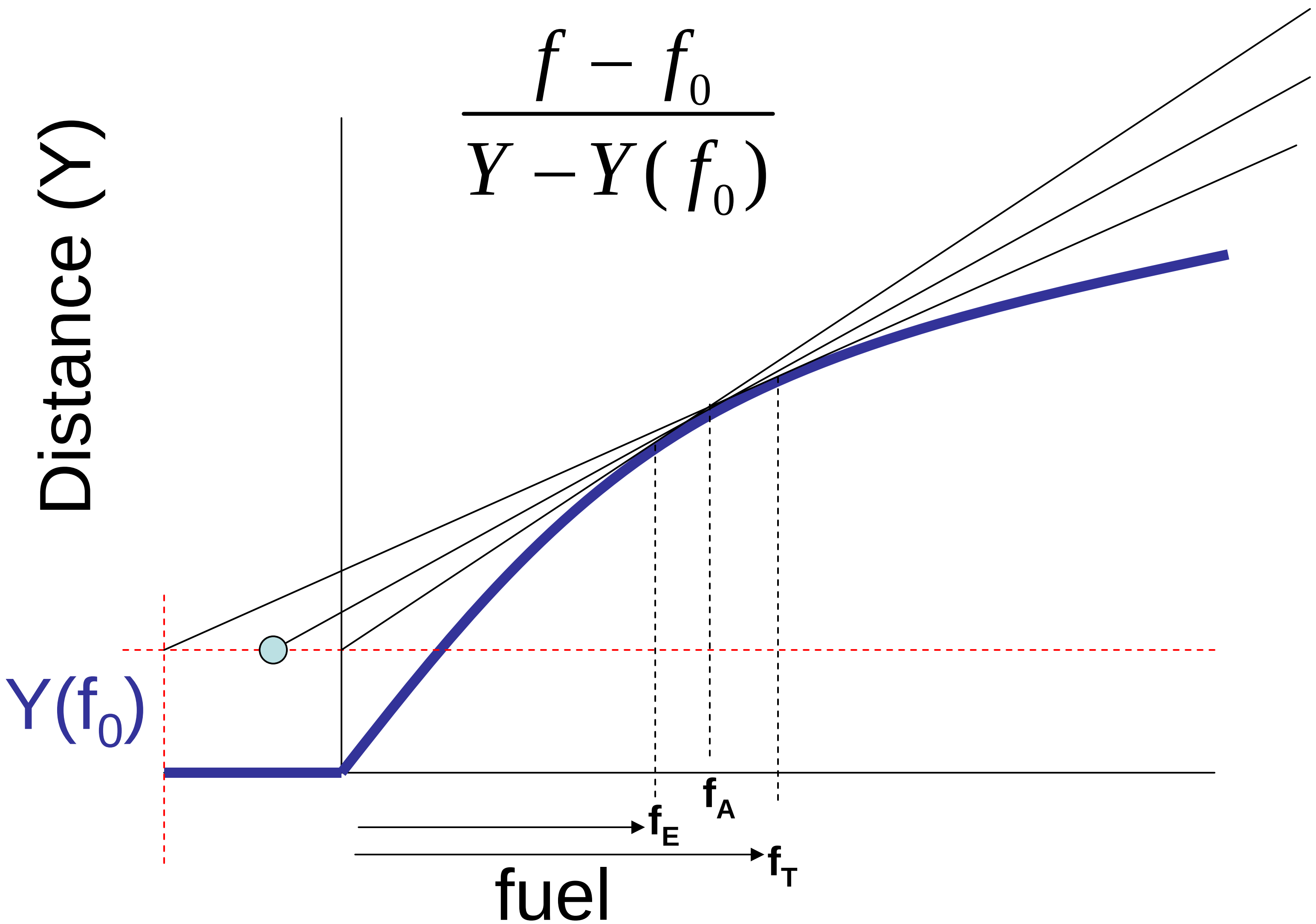
minimize fuel per unit distance: $\dfrac{f}{Y - Y(f_0)}$



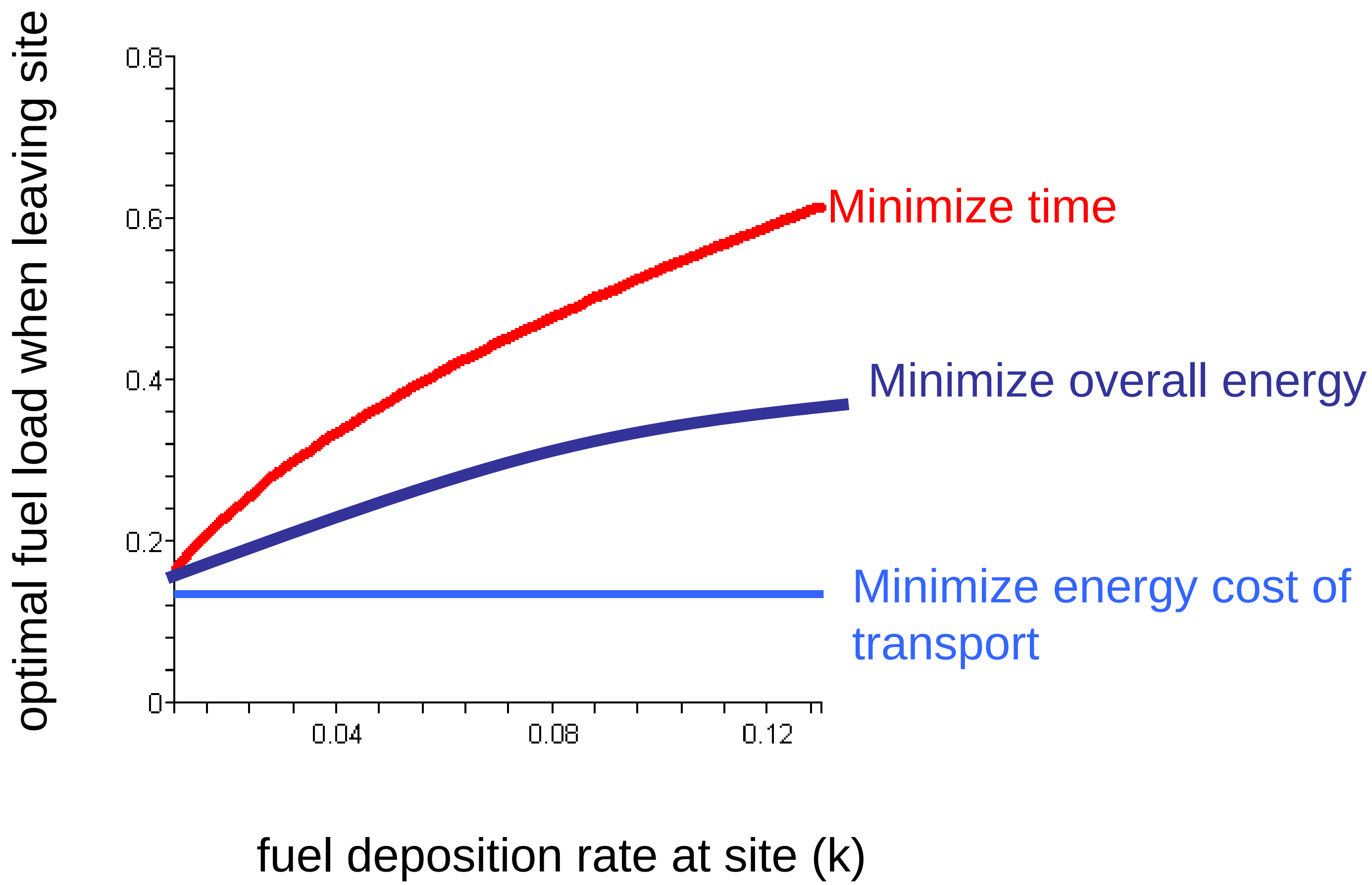
Minimize energy cost of transport



Minimize overall energy



Predictions from theory



Testing the theory

- 9 tests
  - 7/9 show significantly positive relationship between departure fuel and k
  - strong support for time-selected migration in birds from experimental tests

(Hedenstrom 2008)

Other predictions

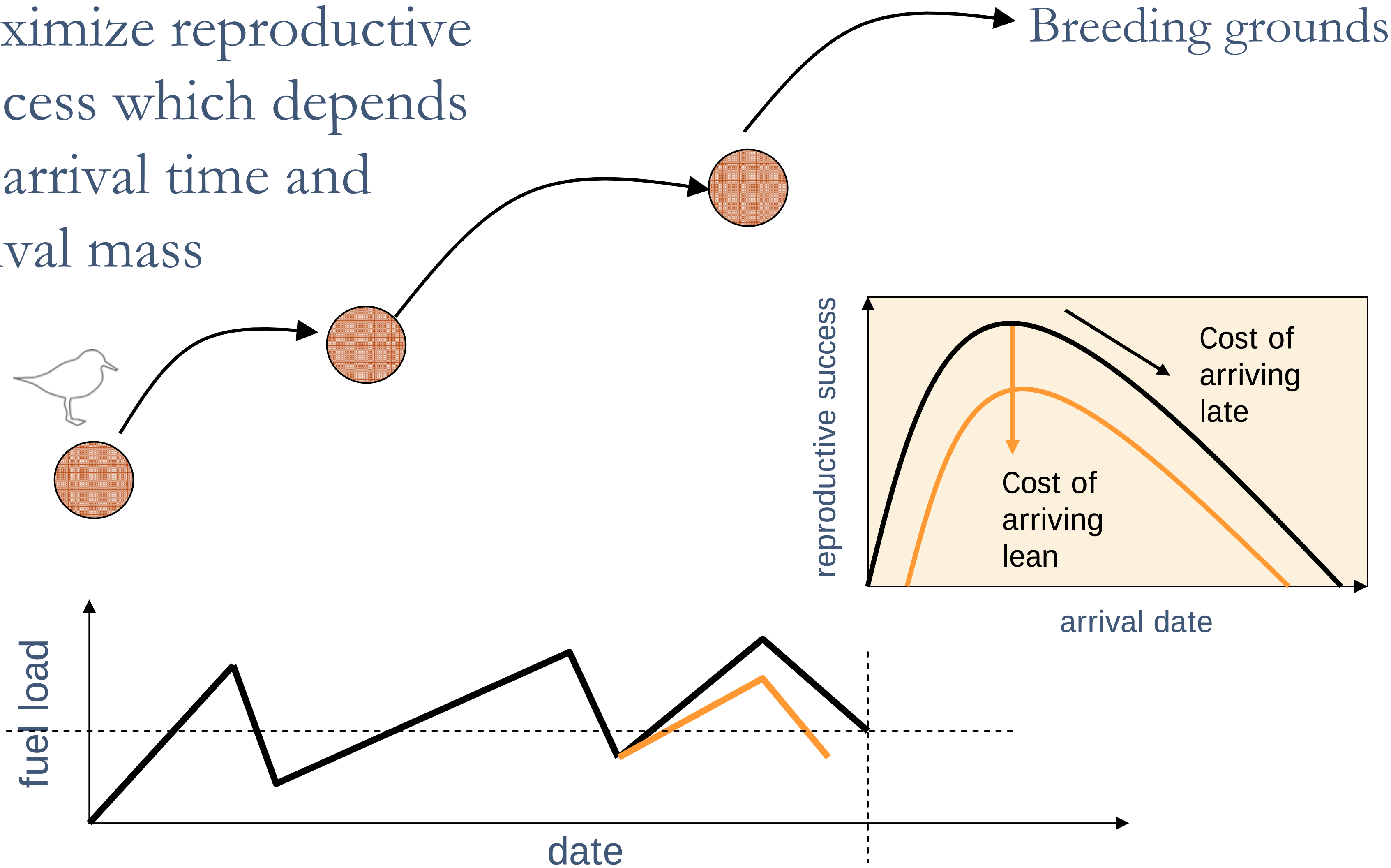
- flight speed should vary depending on currency, optimal flight speed is greater for time-selected migrants than for energy selected
- greater physiological flexibility expected in time-selected migrants (Weber and Hedenstrom 2001)

What the static optimization theory does not cover

- Refueling sites are limited
- fitness surrogate is a mixture of arrival time and arrival fuel.
- intermediate arrival time is optimal, fitness declines if bird arrives too early as well as too late
- decision to leave site depends on multiple state variables of individual bird

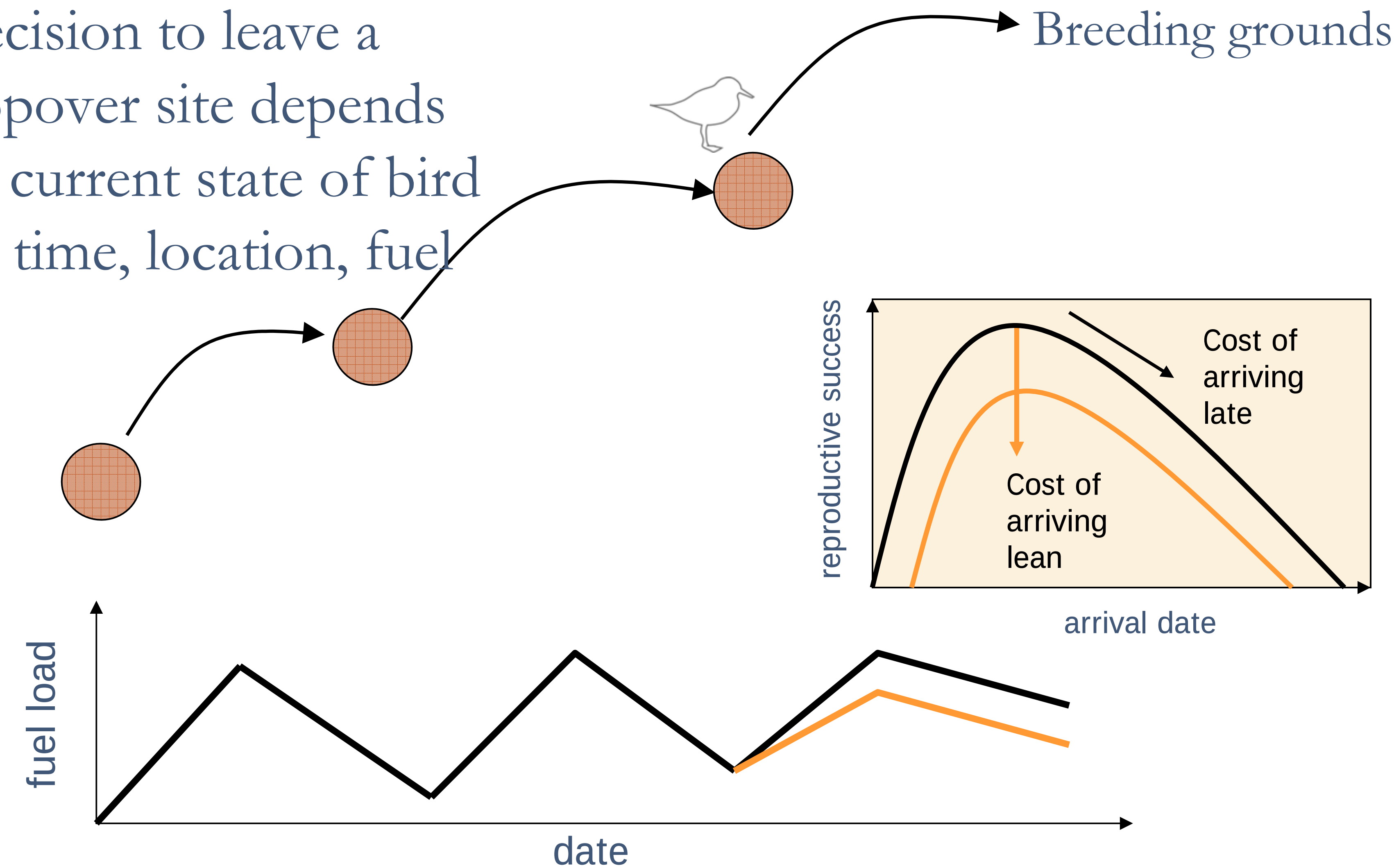
Modeling Migration

Maximize reproductive success which depends on arrival time and arrival mass



Modeling Migration

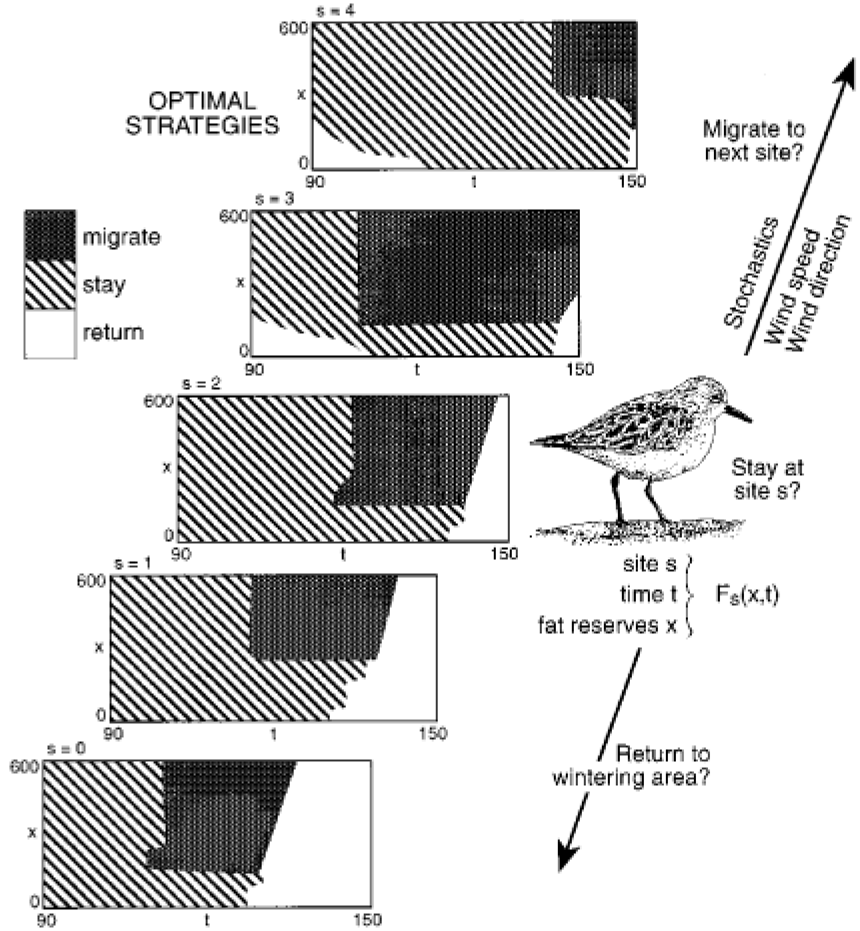
Decision to leave a stopover site depends on current state of bird i.e. time, location, fuel

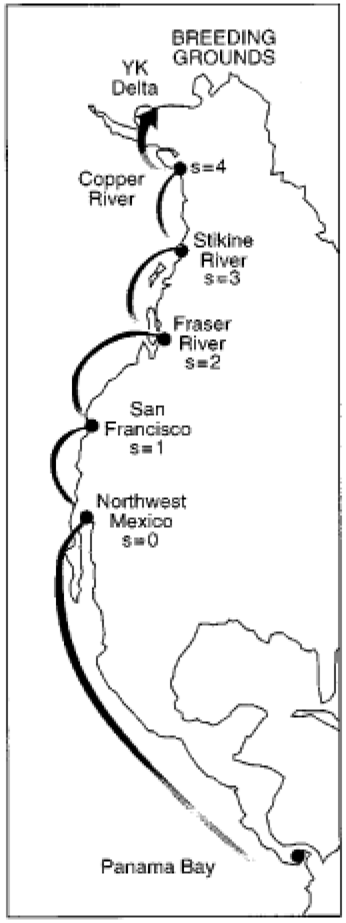


Dynamic state variable approach

- Components of a state variable model are:
  - time horizon and time step
  - state variables
  - decision variables
  - state dynamics and stochastics
  - fitness function for backwards iteration
  - terminal fitness
  - parameters
- Output is:
  - maximum fitness for each possible state and time
  - decision matrix, optimal decision at every possible state and time

Dynamic state variable approach





From: Clark & Butler 1999

Example (very simple) model

- 3 sites
- each time step is 1 day,
- time horizon is 4 days
- Terminal fitness – depends on time and fuel at final site F(t=4,s,x)
- decision variable (Stay or leave)
- state variables Fuel (X), site, time
- state dynamics, costs 1 fuel to migrate, add 1 if stay and forage :
  - X(t+1) = min(2,X(t)+1) if bird stays
  - X(t+1) = X(t) -1 if bird leaves site
- fitness
  - fitness is maximum of (fitness if leave and fitness if stay)
  - F(t,s,x) = max(F(t+1,s+1,x-1),F(t+1,s,x+1))
  - if X(t) < 0 then F = 0
  - if (t = 4 and s = 1 or 2) then F = 0

Terminal fitness at Site 3 :

Fuel

2	0	0.3	0.9	0.6
1	0	0.2	0.7	0.4
0	0	0.1	0.5	0.2
	1	2	3	4

Time

Work backwards to calculate maximum fitness for site 2

Site 2

Maximum fitness:

Fuel

2			?	0
1				0
0				0
	1	2	3	4

Time

Optimal decision:

Fuel

2			S/L	-
1				-
0				-
	1	2	3	4

Time

Terminal fitness at Site 3 :

Fuel				
2	0	0.3	0.9	0.6
1	0	0.2	0.7	0.4
0	0	0.1	0.5	0.2
	1	2	3	4

Time

Work backwards to calculate maximum fitness for site 2

Site 2

Maximum fitness:

Fuel				
2	0.7	0.7	0.4	0
1	0.7	0.5	0.2	0
0	0.5	0.2	0	0
	1	2	3	4

Time

Optimal decision:

Fuel				
2	S	L	L	-
1	S	L	L	-
0	S	S	-	-
	1	2	3	4

Time

Site 3

2	0	0.3	0.9	0.6
1	0	0.2	0.7	0.4
0	0	0.1	0.5	0.2
	1	2	3	4

Site 2

Maximum fitness:

2	0.7	0.7	0.4	0
1	0.7	0.5	0.2	0
0	0.5	0.2	0	0
	1	2	3	4

Optimal decision:

2	S	L	L	-
1	S	L	L	-
0	S	S	-	-
	1	2	3	4

Work backwards to calculate maximum fitness for site 1

Site 1

Maximum fitness:

Fuel

2				0
1				0
0				0
	1	2	3	4

Time

Optimal decision:

Fuel

2				-
1				-
0				-
	1	2	3	4

Time

Site 3

2	0	0.3	0.9	0.6
1	0	0.2	0.7	0.4
0	0	0.1	0.5	0.2
	1	2	3	4

Maximum fitness:

Site 2

2	0.7	0.7	0.4	0
1	0.7	0.5	0.2	0
0	0.5	0.2	0	0
	1	2	3	4

Optimal decision:

2	S	L	L	-
1	S	L	L	-
0	S	S	-	-
	1	2	3	4

Work backwards to calculate maximum fitness for site 1

Site 1

Maximum fitness:

Fuel

2	0.5	0.2	0	0
1	0.2	0	0	0
0	0	0	0	0
	1	2	3	4

Time

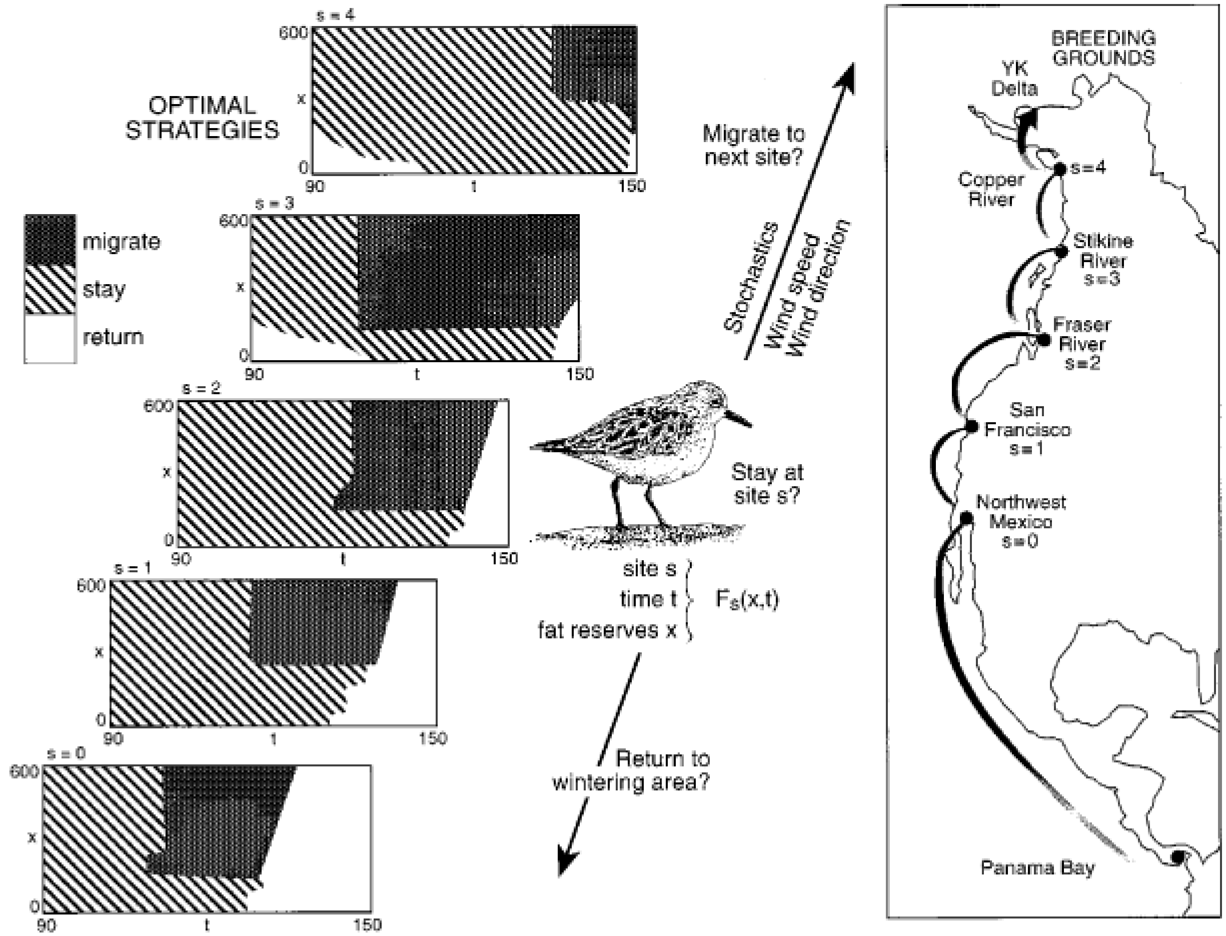
Optimal decision:

Fuel

2	L	L	-	-
1	S/L	-	-	-
0	-	-	-	-
	1	2	3	4

Time

Dynamic state variable approach



From: Clark & Butler 1999

Uses of state-variable migration models

- forward-simulation to generate predictions

- re-generate decision matrices with different environmental conditions.

- compare results from different forward simulations

Uses of state-variable migration models

•consequences of different fitness measures (Weber et al. 1998)
•decline in habitat quality (Weber et al. 1999)
•spacing and availability of stopover sites (Farmer & Wiens 1998; Farmer & Wiens 1999);
•environmental stochasticity in fuel deposition rate, wind and predation (Weber et al. 1998).
•State variable models have been applied to real species and give good predictions of observed patterns (Clark & Butler 1999; Farmer & Wiens 1999; Klaassen et al. 2006)
• used to address conservation questions about the effects of anthropogenic actions on bird migration (Klaassen et al. 2006).

References (1)

- Alerstam, T. (1991) Bird Flight and Optimal Migration. Trends in Ecology & Evolution, 6, 210-215.
- Alerstam, T. & Hedenstrom, A. (1998) The development of bird migration theory. Journal of Avian Biology, 29, 343-369.
- Alerstam, T. & Lindstrom, A. (1990). Optimal bird migration: The relative importance of time, energy and safety. In Bird Migration: The physiology and ecophysiology (ed E. Gwinner), pp. 331-351. Springer, Berlin.
- Clark, C.W. & Butler, R.W. (1999) Fitness components of avian migration: A dynamic model of Western Sandpiper migration. Evolutionary Ecology Research, 1, 443-457.
- Clark, C.W. & Mangel, M. (1999) Dynamic state variable models in ecology Oxford University Press Inc., New York.
- Farmer, A.H. & Wiens, J.A. (1998) Optimal migration schedules depend on the landscape and the physical environment: a dynamic modeling view. Journal of Avian Biology, 29, 405-415.
- Farmer, A.H. & Wiens, J.A. (1999) Models and reality: Time-energy trade-offs in pectoral sandpiper (Calidris melanotos) migration. Ecology, 80, 2566-2580.
- Houston, A.I., Clark, C.W., McNamara, J.M., & Mangel, M. (1988) Dynamic models in behavioural and evolutionary ecology. Nature, 332, 29-34.
- Klaassen, M., Bauer, S., Madsen, J., & Ingunn, T. (2006) Modelling behavioural and fitness consequences of disturbance for geese along their spring flyway. Journal of Applied Ecology, 43, 92-100.
- Klaassen, M. & Lindstrom, A. (1996) Departure fuel loads in time-minimizing migrating birds can be explained by the energy costs of being heavy. Journal of Theoretical Biology, 183, 29-34.
- Liechti, F. & Bruderer, B. (1998) The relevance of wind for optimal migration theory. Journal of Avian Biology, 29, 561-568.
- Lindstrom, A. & Alerstam, T. (1992) Optimal Fat Loads in Migrating Birds - a Test of the Time-Minimization Hypothesis. American Naturalist, 140, 477-491.

References (2)

- Weber, T.P. (1999) Blissful ignorance? Departure rules for migrants in a spatially heterogeneous environment. Journal of Theoretical Biology, 199, 415-424.
- Weber, T.P., Alerstam, T., & Hedenstrom, A. (1998) Stopover decisions under wind influence. Journal of Avian Biology, 29, 552-560.
- Weber, T.P., Ens, B.J., & Houston, A.I. (1998) Optimal avian migration: A dynamic model of fuel stores and site use. Evolutionary Ecology, 12, 377-401.
- Weber, T.P., Fransson, T., & Houston, A.I. (1999) Should I stay or should I go? Testing optimality models of stopover decisions in migrating birds. Behavioral Ecology and Sociobiology, 46, 280-286.
- Weber, T.P. & Hedenstrom, A. (2000) Optimal stopover decisions under wind influence: the effects of correlated winds. Journal of Theoretical Biology, 205, 95-104.
- Weber, T.P. & Houston, A.I. (1997) Flight costs, flight range and the stopover ecology of migrating birds. Journal of Animal Ecology, 66, 297-306.
- Weber, T.P. & Houston, A.I. (1997) A general model for time-minimising avian migration. Journal of Theoretical Biology, 185, 447-458.
- Weber, T.P., Houston, A.I., & Ens, B.J. (1994) Optimal Departure Fat Loads and Stopover Site Use in Avian Migration - an Analytical Model. Proceedings of the Royal Society of London Series B-Biological Sciences, 258, 29-34.
- Weber, T.P., Houston, A.I., & Ens, B.J. (1999) Consequences of habitat loss at migratory stopover sites: a theoretical investigation. Journal of Avian Biology, 30, 416-426.