WLF 419 - Waterfowl and Wetlands Ecology and Management
Lecture 11 – Breeding Parameters
Next Time – Survival

Breeding probability (propensity), clutch size, and nest success are the main parameters that determine reproductive performance of waterfowl. We will examine approaches to studying these parameters and the range and source of variation in these parameters.

Breeding probability (Age of reproductive maturity, first reproduction) – probability that a bird alive at breeding season *i* will breed

Breeding propensity - probability that a bird alive at breeding season *i* will breed, given that it bred in a previous season

Breeding Probability (accepted values)

- Species-specific, but shaped by ecological factors
  - Anatini – yearlings
  - Aythini –yearlings or 2-year-olds
  - Mergini and Anserini – 2- or 3-year-olds
    - Recent evidence of nesting by yearling Canada geese (physiological limitations?)
  - Cygnini – 3-year-olds
    - Proportion of breeders for Mute Swans (Perrins and Reynolds 1967)
      - 10.5%, 3-year-olds
      - 37%, 4-year-olds
      - 53%, 5-year-olds
      - 71%, 6-year-olds

Timing of Breeding

- Latitudinal variation
- Age
  - Younger birds nest later
- Condition
  - Mostly indirect evidence (e.g., winter severity and timing of nesting)
- Experience?

- Difficult to separate from experience
- Habitat Conditions
  - Drought
  - Ice
  - Drought Displacement
- Weather
  - Boom and Bust for Northern Geese

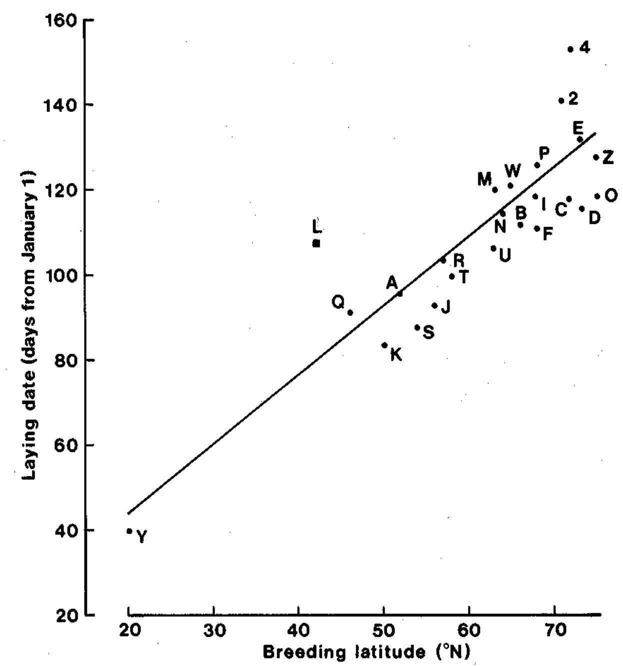


Figure 18 The relationship between the mean date of the laying of the first egg at Slimbridge and the mid-latitude of the breeding range in the wild. Letters refer to Appendix I. The correlation and the regression line excludes the Bar-head (L) because it breeds at high altitude. The Red-breasted Goose (4) is exceptional for other reasons (see text), $r = 0.913$ $P < 0.001$

From Owen (1980)

Renesting and Double Brooding

- Renesting – nesting that occurs after an earlier clutch is destroyed or abandoned in the same season
  - Does not occur in northern nesting geese
  - 5 breeding attempts by some prairie nesting ducks
  - Renesting Interval
- Double Brooding – attempt to produce second clutch after one has hatched successfully in the same year

- Wood Ducks
- Evidence for low latitude Canada geese, Redheads, Mallards, and Pintails

Breeding Propensity

- Limited Information
- Reproductive Restraints vs. Reproductive Constraints for Young Birds
  - Survival Costs
  - Restraint
    - Young Goldeneyes laying early or larger clutches disappeared from population in subsequent years (Dow and Fredga (1984)
    - Lesser Snow Geese
      - Geese breeding for the 1st time are 22% less likely to be seen the next year than birds in later breeding attempts

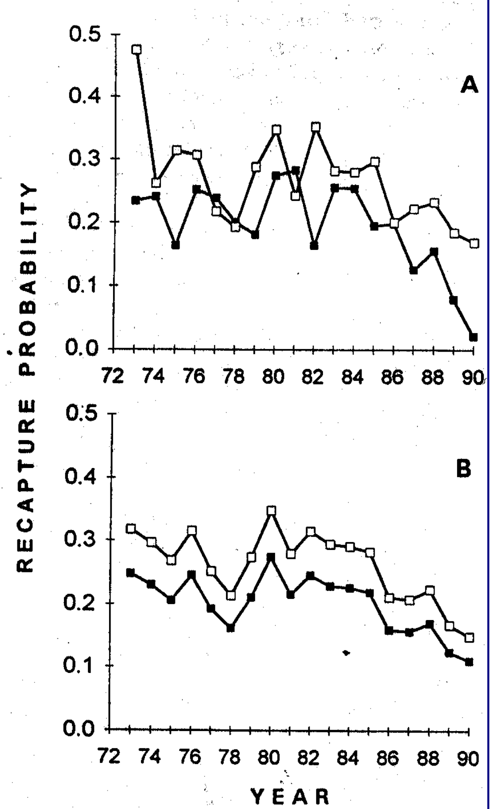


Fig. 1. Estimates of recapture rates after first breeding (■) or after later recapture occasions (□) under (A) model ϕ_t, $p_{t \cdot F}$ and (B) model ϕ_t, p_{t+F} for all birds.

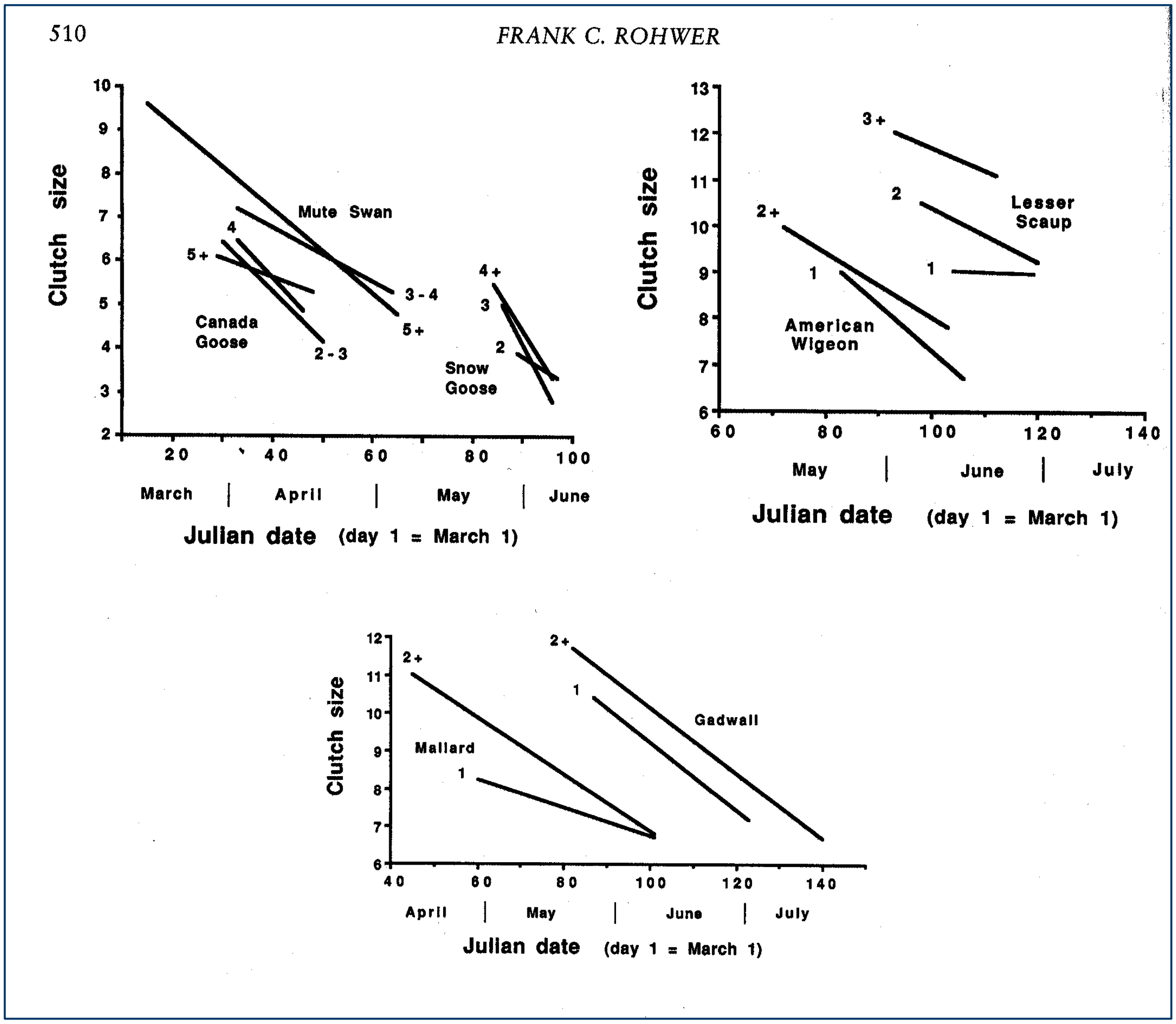
From Viallefont et al. (1995)

- Adults
    - Life-history tradeoffs or Good vs. Bad Bird
        - Canvasbacks (Lindberg et al. 2001)
            - Probability of presence for birds that breed in previous year – 0.959
            - Probability of presence for birds that didn't breed the previous year – 0.595
    - Habitat and Weather
        - Drought displacement
        - Boom and bust
    - Competition/Density
        - Black Brant
        - Black Ducks and Mallards?

Clutch Size

- Species-specific variation
    - Related to a variety of factors
    - Cygnini, 3-5 eggs, clutches of 1-9 eggs reported for Trumpeters
    - Anserini, 3-5, a few with 6-7 eggs
    - Dendrocygninae, average about 12, 6-18 reported
    - Aythyini, typically 9 or 10 eegs
    - Oxyurini, 4-6 eggs
    - Anatini and Mergini
        - Large variaion
        - Widely distributed

- Proximate Factors
    - Season Decline
        - Universal
    - Age



From Rohwer (1993)

- Condition of the female
    - Drent and Daan (1980) – prudent parent
    - Smaller clutches optimal for some members of the population
        - Reduced survival with larger clutches

- Ultimate Regulation
    - Timing of Nesting
    - Competing hypotheses
        - Incubation-energetics
        - Laying-delay
        - Optimal-rearing
        - Predation
        - Nest-site

- Clutch Size
  - Lack – The optimum clutch size is the most common clutch size, producing the most surviving young for a breeding attempt
  - Maximizing output at each breeding attempt instead of over the lifetime of the bird (LRS)
  - Increased output at the current breeding attempt could reduce LRS
  - Food limitation for altricial birds?
    - Predation may be more important
    - Does not work for precocial species with self-feeding young
  - Precocial
    - Brood Size
    - Egg production
      - Egg size
      - Nutrient
    - Egg Viability, Predation, Synchrony
  - Hypotheses for Seasonal Decline
    - Territory Quality
    - Parent Quality
    - Food Decline

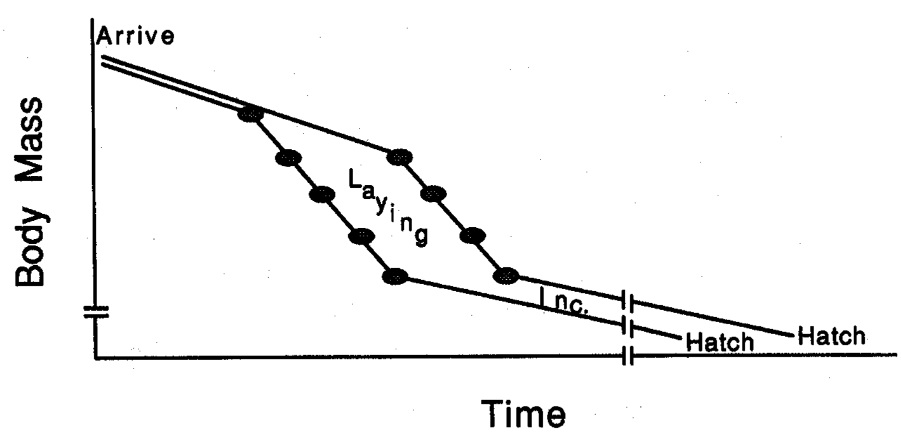


Figure 15-10. Graphical model of the nutrient-reallocation hypothesis for seasonal declines in clutch size. The individual that delayed nesting could lay only 4 eggs because stored nutrients were used to meet maintenance requirements. In the purest form of this model, all individuals arrive together and have the same level of nutrient reserves at arrival and again at the end of laying.

From Rohwer (1993)

- Synchrony
- Cost-of-delay

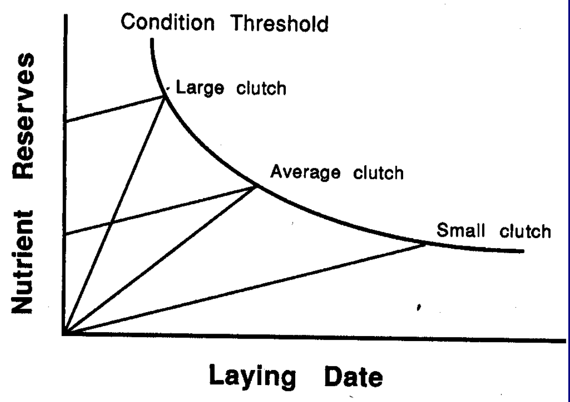


Figure 15-11. Graphical model of the seasonal change in the threshold of nutrient reserves required for nest initiation (after Reynolds 1972). This model assumes that nutrient reserves directly affect clutch size. The *diagonal lines* represent rates of nutrient storage. Females' conditions could differ because they have differing rates of nutrient storage (*the three lines coming out of the origin*), because they have equal rates of nutrient storage (*the three parallel lines with differing intercepts*), or both.

(From Rohwer 1993)

- Changes-in-cost-of-reproduction

- Nest Success
  - Most studied population parameter
  - Low with large Annual, Spatial, and Species-specific variation
    - Predation
  - Variation
    - Age, Experience, Condition
    - HABITAT
    - Density and Parasitism
    - Humans and Weather

- Egg Survival
  - Infertiliy
  - Embryonic Death
  - Predation

Table 4. Estimated percent nest success, number of nests (*n*), and percent of nest initiations (I) by habitat for mallard, gadwall, blue-winged teal, northern shoveler, and northern pintail in North Dakota, 1966–84.

Habitat Period	Mallard			Gadwall			Blue-winged Teal			Shoveler			Pintail		
	%	*n*	I	%	*n*	I	%	*n*	I	%	*n*	I	%	*n*	I
Cropland															
1966–74	1	5	7	20	6	3	6	26	5	7	3	3	5	53	51
1975–79	2	10	9	24	0	4	7	1	6	9	6	4	6	27	57
1980–84	3	4	9	41	1	4	12	6	6	15	0	4	11	27	57
Hayland															
1966–74	2	0	9	3	1	10	7	4	5	2	0	5	2	0	6
1975–79	4	31	12	6	20	13	13	29	7	4	3	6	3	10	6
1980–84	6	11	12	8	27	13	18	25	7	6	12	6	4	12	6
Grassland															
1966–74	6	17	23	12	53	31	11	233	43	14	11	39	10	16	21
1975–79	12	116	27	23	96	35	21	524	48	27	72	46	19	70	21
1980–84	8	76	26	15	127	35	14	201	47	18	63	46	13	69	21
Idle grassland															
1966–74	18	59	<1	18	142	<1	11	469	<1	16	35	<1	18	30	<1
1975–79	27	253	1	26	230	1	17	480	1	22	42	<1	27	66	<1
1980–84	27	466	1	27	313	1	17	437	1	22	69	<1	27	89	<1
Planted cover															
1966–74	10	156	28	14	202	26	13	405	20	12	41	25	10	105	13
1975–79	10	660	11	13	740	10	13	1,608	7	12	336	9	10	454	4
1980–84	9	272	11	12	377	11	12	482	8	11	96	10	9	97	5
Right-of-way															
1966–74	4	11	4	7	12	3	11	24	3	6	3	4	6	5	2
1975–79	5	63	5	10	39	4	15	148	3	9	33	5	9	45	2
1980–84	5	57	5	9	31	4	13	50	3	8	13	5	8	8	2
Wetland															
1966–74	7	2	13	10	4	15	11	44	13	3	0	13	5	6	4
1975–79	7	20	15	9	8	18	10	43	14	3	4	15	5	2	4
1980–84	12	37	15	16	28	18	17	51	14	5	14	15	8	8	4
Odd area															
1966–74	5	6	16	17	5	11	14	21	11	9	1	11	6	1	4
1975–79	5	41	20	18	20	15	15	60	14	10	7	14	7	13	4
1980–84	3	26	20	12	22	15	10	22	14	7	7	14	5	6	4
Total															
1966–74	6	256	100	12	425	100	11	1,226	100	10	94	100	7	216	100
1975–79	8	1,194	100	16	1,153	100	17	2,893	100	16	503	100	9	687	100
1980–84	7	949	100	15	926	100	14	1,274	100	13	274	100	10	316	100

From Klett et al. (1988)

Table 22. Mayfield estimates[a] of nest success of duck nests on Minto Flats, Alaska in 1989, 1990 and 1991, and years combined.

Species[b]/Year	No. hatch	No. fail	exposure days	DSR[c]	success %	95%CI
1989						
Northern pintail	9	17	188	0.910	6.4	2-24
Mallard	10	16	261	0.939	10.3	3-32
Northern shoveler	25	29	557	0.948	17.1	9-33
American wigeon	8	12	216	0.945	16.1	6-46
Scaup	8	27	295	0.909	3.5	1-12
1990						
Northern pintail	16	40	382	0.895	4.1	2-11
Mallard	13	20	327	0.939	9.7	3-27
Northern shoveler	32	81	825	0.902	3.3	2-7
American wigeon	7	20	231	0.914	5.5	2-20
Scaup	19	45	462	0.903	2.8	1-8
Canvasback	8	8	96	0.917	5.7	1-41
1991						
Northern pintail	6	32	265	0.879	2.4	1-9
Mallard	20	35	634	0.945	13.0	7-26

Table 22. Continued.

Species[b]/Year	No. hatch	No. fail	exposure days	DSR[c]	success %	95%CI
Northern shoveler	22	59	598	0.902	3.3	1-8
Green-winged teal	6	9	135	0.934	11.9	3-48
American wigeon	12	20	320	0.938	12.7	5-32
Scaup	28	62	811	0.924	6.2	3-13
All Years[d]						
Northern pintail	31	89	834	0.893	3.8	2-8
Mallard	43	71	1223	0.942	11.6	7-19
Northern shoveler	79	169	1982	0.915	5.3	3-8
Green-winged teal	12	20	315	0.937	13.5	6-33
American wigeon	27	52	768	0.932	10.6	6-20
Gadwall	7	12	179	0.933	9.5	2-36
Scaup	55	134	1569	0.915	4.4	3-8
Canvasback	16	9	191	0.953	21.3	8-59

[a] Johnson 1979.

[b] Only species with > 10 nests/year were listed separately.

[c] Daily survival rate.

[d] Includes species with < 10 nests/year.

From Petrula (1994)

Table 14-2. Reported incidence of egg loss in successful nests of waterfowl species

Species/ Subspecies	Area	Sample size (number of eggs)	Percentage loss to: Infertility	Embryo death	Other	Source
Black Swan	Aust.	1,976			10.3[a]	Braithwaite 1982
Graylag Goose	Scot.	373			6.0[a]	Newton & Kerbes 1974
Bar-headed Goose	Ger.	All nests[b]	7.0	49.5	15.5	Lamprecht 1986
Snow Goose	N.W.T.	403	1.0		29.8	Ryder 1971
Ross' Goose	N.W.T.	2,235		3.5-6.6[a]	13.1-33.2	Ryder 1972
Emperor Goose	AK	1,303	2.5	0.3	20.4	Eisenhauer & Kirkpatrick 1977
Canada Goose	BC	1,907[b]	1.8	2.2	7.2	Munro 1960
	Alb.	400	5.5	4.0	7.6	Vermeer 1970
	BC	348[b]			23.0	Vermeer & Davies 1978
leucopareia	AK	473[b]	3.5	2.2		Byrd & Woolington 1983
maxima	Manit.	2,912[b]	7.9	2.3	22.0	Cooper 1978
	IL	729	3.0	15.2	4.5	Kossack 1950
	IA	1,002		12.9[a]	1.1	Nigus 1979
moffitti	MT	1,221	6.5	2.1	2.9	Geis 1956
	WA	3,947	1.5	6.3	0.6	Hanson & Browning 1959
	WA	14,796	2.6	6.4	2.3	Hanson & Eberhardt 1971
	CA	810	1.9	9.4	1.7	Miller & Collins 1953
	CA	350	2.0			Naylor 1953
	CA	432	2.1			Naylor & Hunt 1954
occidentalis	AK	1,017	0.9	8.3	7.4	Hansen 1961
Wood Duck	NY	644	5.5			Haramis & Thompson 1985
	MA	?	8.0	7.0		McLaughlin & Grice 1952
	OR	640 (dump)		9.2[a]	12.0	Morse & Wight 1969
		261 (normal)		0.8[a]	3.5	
	CA	121 (dump)			47.1	Robinson 1958
		69 (normal)			20.3	
Gadwall	CA	21	4.8			Anderson 1957
	ND	90N[c] (islands)		16.0[a]		Hammond & Mann 1956
		934 (mainlands)	4.8[a]			
	CA	3,834	1.1	3.3	1.4	Miller & Collins 1954
	CA	2,650	1.8	3.7	1.8	Rienecker & Anderson 1960
	Alb.	259			4.6	Vermeer 1968
Mallard	CA	739	3.7	5.0	7.9	Anderson 1957
	Que.	793	2.3		9.7	Laperle 1974
	Pol.	1,278[b] (nest basket)	1.0			Majewski 1986
		330[b] (natural nest)	0.9			

nated with chlorinated hydrocarbons. Blus et al. (1979) ...

Table 14-2. Reported incidence of egg loss in successful nests of waterfowl species (continued)

Species/ Subspecies	Area	Sample size (number of eggs)	Percentage loss to: Infertility	Embryo death	Other	Source
Mallard	CA	1,622	1.6	4.9	2.1	Miller & Collins 1954
	CA	2,804	1.4	4.5	1.9	Rienecker & Anderson 1960
	FL	612	2.8	0.3	3.3	Stieglitz & Wilson 1968
Black Duck	Que.	484	2.2		11.4	Laperle 1974
	MD	336	0.3	2.1		Stotts & Davis 1960
Pintail	CA	376	1.9	5.1	0.7	Miller & Collins 1954
	CA	1,556	3.7	4.4	1.3	Rienecker & Anderson 1960
Cinnamon Teal	CA	64	9.4	4.7	12.5	Anderson 1957
	CA	343	0.9	9.0	1.7	Miller & Collins 1954
	CA	287	1.0	8.4	0.7	Rienecker & Anderson 1960
N. Shoveler	CA	389	1.3	4.4	2.8	Miller & Collins 1954
	CA	657	0.8	3.8	1.0	Rienecker & Anderson 1960
Canvasback	OR	375	8.0 (host)	5.1 (host)		Erickson 1948
E. Pochard	Czech.	1,056		9.8[a]	0.3	Havlín 1966a
Redhead	IA	97	25.7			Bennett 1938
	MT	202	3.5	6.9	20.8	Lokemoen 1966
	IA	1,509[b]	4.7	5.5		Low 1945
	CA	303	3.0	24.8	3.6	Miller & Collins 1954
	CA	892	5.0	21.4	0.8	Rienecker & Anderson 1960
Tufted Duck	Czech.	1,050		10.8[a]	1.1	Havlín 1966a
Lesser Scaup	CA	96	2.1	10.4		Miller & Collins 1954
	CA	209		4.8	7.2	Rienecker & Anderson 1960
	Alb.	619			9.0	Vermeer 1968
Eider	Neth.	?			4.0[a]	Swennen 1983, citing Bergman 1939
Bufflehead	BC	751	2.5	2.1	2.1	Erskine 1971
H. Merganser	Que.	173		8.7[a]		Bouvier 1974
Goldeneye	Que.	37		13.5[a]		Bouvier 1974
Ruddy Duck	IA	546[b]	1.5	5.5	0.7	Low 1941
	CA	64		28.1	1.5	Miller & Collins 1954
	CA	268	2.6	22.8	0.8	Rienecker & Anderson 1960

[a]Value includes percentage loss to infertility and embryo death.
[b]The sample size refers to eggs from successful and unsuccessful nests.
[c]N pertains to the number of nests rather than the number of eggs.

From Johnson et al. (1993)

Approaches to Estimation

Nest Success

- Convergent Evolution
    - Medical research and those studying nest survival
    - Mayfield
        - Apparent nest success = # destroyed / number found
            - Violates the assumption that marked population is representative of unmarked population
            - More likely to find long-lived nest than those destroyed early in incubation
            - Overestimate (bias) of nest success or nest survival
                - Solutions
                    - Include only nests found on 1st day of laying
                    - Use Mayfield Estimator, *adhoc estimator*

$$\hat{S} = \frac{(E - f)}{E}$$

where, E is exposure days and f is # of failures (mortalities)

Mayfield Model

- What is the nest survival for the Ruddy Duck during laying and incubation?
- Assumes constant daily survival probability

	Days					**Start of Study (Day)**	
Nest	**0**	**3**	**6**	**9**	**12**	**3**	**9**
1.	0	X	X	X	X		
2.	0	0	0	0	0	U	U
3.	0	0	0	X	X	U	
4.	0	X	X	X	X		
5.	0	0	0	X	X	U	
6.	0	X	X	X	X		
7.	0	0	X	X	X	U	
8.	0	X	X	X	X		
9.	0	0	0	0	0	U	U
10.	0	0	0	0	X	U	U

- Incubation period = 12 days
- We check nests every 3 days
- 10 nests in our population
- 0 = active nest
- X = nest that failed sometime between sampling occasions
- Nests that fail cannot be found

True nest survival = # successful nests / total # of nests = # 0's on day 12 / # nests = 2/10 = 0.2

Start on day 3

Apparent nest survival = # of 0's on day 12/ # of nests that can be found on day 3 = 2/6 = 0.33

Start on day 9

Apparent nest survival = 2/3 = 0.66

Why is apparent nest survival biased?

- Short lived nests are under-represented in the sample
- Marked sample is not representative of the unmarked sample.

Possible Solutions.

- Use only nests with complete histories (reduces sample size).
- Use period-specific estimates.
- Use Mayfield Method or preferable modified Mayfield based on likelihood theory.

Mayfield Method.

- Nest-day = unit of exposure (nest-day is sampling unit not the nest)
- Thus, a nest that survives 3 days = 3 units of exposure
- Mid-point assumption - nest failure assume to occur at mid-point of sampling interval
- Constant DSR

Start on day 3

Mayfield nest survival (DSR) = (9+4.5+4.5+1.5+9+7.5 - 4) / 36 = 0.888
12 day survival probability (Incubation) = 0.888^{12} = 0.24

Start on day 9

Mayfield nest survival (DSR) = (3+3+1.5 - 1) / 7.5 = 0.866
12 day survival probability (Incubation) = 0.866^{12} = 0.18

Disadvantages

- mid-point assumption
- No theoretical basis (no measure of precision)
- Improved by (Johnson 1979 and Bart and Robson 1982)

Breeding Probability and Breeding Propensity

- Marked Birds
  - Capture Histories
- Can You observe breeders and non-breeders?
  - Multistate models
- How do you detect non-breeders when you are generally studying breeding birds?
  - Ratio of detection probabilities

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