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FOOD LIMITATION AND THE ADAPTIVE SIGNIFICANCE OF CLUTCH SIZE IN AMERICAN COOTS (Fulica americana)

by

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Submitted in partial fulfilment
of the requirements for the degree of
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FOOD LIMITATION AND THE ADAPTIVE SIGNIFICANCE OF CLUTCH SIZE IN AMERICAN COOTS (*Fulica americana*).

For many species of birds, egg formation costs are considered important constraints on timing of breeding, clutch size, and egg size. For American Coots (*Fulica americana*), body reserves and current food availability are both thought to affect these aspects of reproduction. In order to test the egg formation hypothesis, I conducted numerous observational and manipulative experiments on wild, free-ranging American Coots. Clutch size declined with laying date in five out of six years, contrary to seasonal patterns of food availability in prairie wetlands. Clutch size increased during two of three years in response to supplemental feeding. Laying date was only slightly affected by food supplements. Coots renested rapidly following clutch destruction, and some females produced phenomenal numbers of consecutive or near-consecutive eggs (to a maximum of 35 in 37 d). Because the average clutch was usually 8 - 11 eggs, these data provided a strong refutation of the egg formation hypothesis.

Egg size exhibited little change in response to most factors, and egg composition was only slightly more sensitive to such factors as annual variation and supplemental feeding. Egg size and quality (relative protein, lipid, and energy content) were positively correlated with clutch size, contrary to predictions based on life-history trade-offs. I suggest that among-individual variation in "inherent quality" overshadows these expected trade-offs.

Analysis of nutrient reserve dynamics of adult coots did not support earlier claims that coots rely on stored fat and protein for egg production. In general, coots exhibited little sign of nutritional stress during breeding, although supplemental feeding did result in increased fat and protein reserves. Among postlaying female coots, there were significant positive correlations between size of reserves and measures of previous reproductive performance. These observations lend further support to the idea that individual females are inherently "superior" or "inferior" breeders, but they do not give any indication why this might be so.

I conclude that coots are not food limited during egg laying or incubation. Further work is needed on the potential role of food limitation during brood-rearing, particularly with regards to variation in brood size and hatching asynchrony.

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CHAPTER 1. GENERAL INTRODUCTION

1.1 OVERVIEW

According to David Lack (1947*a*, 1954), food availability was the major environmental constraint shaping the life-history strategies of animal populations. Hence, for most invertebrates and lower vertebrates, Lack suggested that reproductive rates were limited by the amount of food resources that could be channeled into egg formation (Lack 1954). Much of the interspecific variation in number of eggs produced per breeding event was assumed to be related to egg size; i.e., with a fixed amount of food resources, a species could produce many small eggs or a few big eggs (Lack 1954). For species that provisioned their newly hatched/newly born offspring (i.e., most birds and mammals), Lack suggested that brood/litter size was constrained by the ability of parents to provide food for their dependent offspring, and not by the ability of parents to form eggs or embryos (Lack 1947*a*, 1948*c*). Because all populations were assumed to be reproducing at the fastest rate possible (as determined by food availability), and because populations were assumed to fluctuate only within narrow limits, Lack viewed mortality rates as a density-dependent consequence of reproductive rates (Lack 1947*a*, 1954). Mortality of mature individuals was assumed, among most higher vertebrates, to be caused by food shortage (i.e., starvation) during the non-breeding season (Lack 1954, 1966).

Although Lack recognized other factors such as predation, parasites, disease, climate, and population density *per se* that could limit animal populations, with few exceptions (i.e., herbivorous insects, ungulates, and grouse) he assigned these factors only minor importance in comparison to food limitation (Lack 1954, 1966). Lack's views were not without their critics: Wynne-Edwards (1962, 1963) proposed that inter-group selection was responsible for molding life-history tactics such that food limition would rarely occur (similar explanations were presented by Moreau 1944, Skutch 1949, and Wagner 1957; but without a mechanism [i.e., group selection] by which they might have evolved), Andrewartha and Birch

(1954) stressed the importance of density-independent factors such as severe weather in regulating populations (particularly of insects), Chitty (1967) and Watson (1967) championed the hypothesis of social (territorial) regulation of populations, and several recent writers have advocated that predation regulates population numbers and/or reproductive rates well below the limits that might be set by food availability (Erlinge *et al.* 1984, Sinclair 1985, Krebs *et al.* 1986, Arnold *et al.* 1987, George 1987, Lima 1987, Trostel *et al.* 1987).

Most of Lack's ideas were derived from studies of the reproductive ecology of birds (e.g. Lack 1946; 1947*a,b*, 1948*a,b*), and these ideas were only secondarily applied to other taxa (Lack 1948*c*, 1954). In this thesis, I intend to critically re-evaluate Lack's hypothesis that food availability is the primary factor limiting reproductive rates in birds.

1.1.1 *Food as a Limit to Reproductive Rates in Birds: an Historical Perspective.*

One of the first investigators to provide a thorough examination of variation in reproductive rates (i.e., clutch sizes) of birds from a life-history perspective was R. E. Moreau (1944). Moreau observed that clutch sizes of European birds were much larger than in South African birds, which were in turn larger than clutch sizes of equatorial African birds. Within equatorial Africa, there was also a tendency for birds of the dry savannah to produce larger clutches than birds of the rain-forest. On the basis of several studies of parental feeding rate in relation to brood size (e.g., Moreau 1940, 1941, 1942*a,b in* Moreau 1944), all of which showed that parents with larger broods could increase their feeding rate substantially, Moreau (1944) concluded that food limitation for nestlings was irrelevant (at most, he reasoned, it might fix the upper limit to clutch size among species with variable-sized clutches). He also rejected earlier claims (e.g., Hesse *et al.* 1937) that geographic variation in clutch size was related to daylength (and hence the amount of time parents had to feed their young), because clutch size differed between Europe and South Africa, and between equatorial savannah and equatorial rain-forest, whereas latitude (and hence daylength) clearly did not (Moreau 1944). Moreau therefore suggested that clutch size had evolved to balance the natural mortality rate (which he believed was higher in Europe due to the rigors of annual migration). Moreau (1944: 309) even suggested that this "balance" might be somewhat difficult to detect because birds raising larger broods might also have higher mortality as a result of raising larger broods; i.e., he fully elucidated the "cost of reproduction" hypothesis (variously credited to Lack 1966, Williams 1966, Charnov and Krebs 1974), although Moreau clearly allocated this hypothesis only secondary importance. Moreau (1944) concluded his review of clutch size in African birds by stating: "I recognize, perhaps as fully as anyone else, the inadequacy of the foregoing discussion. All I claim is that I have shown the reality of a problem, immense and fundamental, in population dynamics. I do not believe that single, or simple, explanations will be found."

David Lack was a staunch proponent of the "single and simple explanation;" in an obituary on Lack, one of the only criticisms raised by long-time friend and colleague Ernst Mayr (1973) (himself not exactly renowned as a compromiser) was Lack's refusal to seriously consider multi-factor hypotheses in his research. Although Lack (1947*a*) credited Moreau (1944) for having ignited his interest in clutch size, he dismissed Moreau's "balanced-mortality hypothesis" as an inadvertent (but necessary) consequence of finite population size. Lack's central hypothesis was initially simple: in nidicolous species, the average clutch size was ultimately determined by the average maximum number of young that the parents could successfully provision with food (the "brood-provisioning hypothesis" [my term]; Lack 1947*a*). Hence clutch size increased with latitude, and declined seasonally (i.e., throughout the summer), due to parallel variation in daylength, which affected how much food parents could provide to the nestlings each day (Lack 1947*a*). Clutch size exhibited little annual variation because food supply during the nestling period could not be predicted when the parents were laying eggs, except on a long-term (i.e., ultimate) basis. The exceptions in this case were thought to prove the rule: vole-eating raptors showed pronounced annual variation in clutch size that ran parallel to changes in vole density. In this situation, annual food availability during brood rearing was highly variable, but highly predictable. Lack (1948*b*) also recognized that predation could influence optimal clutch size, but he assumed that predation had only a modifying influence relative to food availability: parents could use the same amount of food to raise a few young fast (under high nest predation) or many young slowly (in safe nesting situations). Lack (1947*a*, 1948*b*, 1954) admitted that his brood-provisioning hypothesis ran into trouble with some birds that produce precocial, self-feeding young: for megapodes (Australian mound-building birds with no incubation or post-hatching parental care) he suggested that clutch size might be constrained by the ability of females to produce eggs, for shorebirds he suggested that incubation capacity might be limiting (he remained skeptical), and for waterfowl he ventured no opinions, regarding their situation as "highly puzzling" (Lack 1947*a*: 329).

Lack's brood-provisioning hypothesis was almost immediately criticized by Skutch (1949), who presented a long list of natural history observations on neotropical birds that were inconsistent with Lack's hypothesis. However, Skutch was unable to provide an alternative mechanism that might explain clutch size of tropical birds by something other than group selection, and his observations were rather quickly dismissed by Lack (1949a). Similar exchanges occurred between Wynne-Edwards (1955, 1959, 1962, 1964) and Lack (1954, 1964, 1966); once again, both authors provided numerous credible (and some not so credible) natural history observations, but only Lack provided a credible evolutionary hypothesis. Lack's hypothesis therefore came to be accepted, not because it better explained available natural history data (which it probably didn't, see below), and not because it better withstood attempts to disprove it via hypothesis testing (which it clearly didn't, see below), but because Lack's arguments were more logically in tune with theoretical models of natural selection (Ydenberg and Bertram 1989).

Contrary to Lack's hypothesis, virtually all observational studies of fledging success in relation to brood size have showed that broods <u>larger</u> than the population average produce the most surviving offspring (Lack 1948*a*, 1949*b*, 1950*b*, 1956, 1966 (Campbell's data); Perrins 1965; Cavé 1968; Bryant 1975; Perrins and Moss 1975; Smith 1981; Birkhead *et al.* 1983; Woolfenden and Fitzpatrick 1984; Finke *et al.* 1987; Rockwell *et al.* 1987; Gibbs 1988; Briskie and Sealy 1989; Gibbons 1989). Several refinements to Lack's brood-provisioning hypothesis have attempted to account for the observation that the most productive brood size seems, in the majority of cases, to be larger than the most common brood size: (1) young fledging from larger broods are undernourished; they fledge at lower weights than do offspring from smaller broods, and they suffer disproportionately higher mortality (the "post-fledging survival hypothesis"; Lack 1947*a*, 1948*a*, Perrins 1965); (2) pairs differ in their ability to raise young, and only the highest quality individuals can raise larger than average broods (the "individual optimization hypothesis"; Perrins and Moss 1975, Högstedt 1980, Loman 1980) (such reasoning was also implicit in early explanations of age-related variation in clutch size, e.g., Lack 1947*a*); (3) parents raising larger than normal broods suffer disproportionate mortality, or reduced future fecundity, and hence they produce fewer surviving offspring in their lifetime than do parents attempting smaller broods (the "cost of reproduction hypothesis"; Moreau 1944, Nelson 1964, Lack 1966, Williams 1966, Charnov and Krebs 1974); and (4) larger broods might result in more surviving offspring, but females are unable to produce that many eggs due to food shortages occurring at the time of egg laying (the "egg formation [or production] hypothesis"; Lack 1956, 1964, 1967, 1968; Perrins 1965, 1970; Ryder 1970; Ankney and MacInnes 1978; Ankney and Afton 1988).

It is apparent from some studies of postfledging survival that undernourished young may survive at a lower rate than well-nourished young (Perrins 1963, 1966; Patterson *et al.* 1988; Krementz *et al.* 1989; but see Hedgren 1981, Ross and McLaren 1981, Woolfenden and Fitzpatrick 1984, Newton and Moss 1986). However, many of the above mentioned studies that found greater productivity among broods that were larger than the mean also assessed offspring survival several months or more after offspring became independent of their parents, thereby negating potential concerns about postfledging survival differences (Lack 1948*a*, Perrins and Moss 1975, Woolfenden and Fitzpatrick 1984; Rockwell *et al.* 1987).

Lack's hypothesis may have placed too much emphasis on the average clutch size for the population. Several subsequent studies have shown that birds which lay larger clutches than the population average are also better able to raise larger broods (Perrins and Moss 1975, Högstedt 1980, Loman 1980, Nur 1986, Pettifor *et al.* 1988), hence, at least some of the increase in fledging success with brood size may be due to inter-individual variation in optimal clutch size within a population. If this hypothesis is valid, then it is inappropriate to test Lack's hypothesis using observational studies: individual brood sizes must be manipulated (Lessells 1986, Nur 1987). Ironically, the earliest brood manipulations that I am aware of were not conducted by advocates of individual selection, they were conducted by "bumbling naturalists" who disagreed almost wholly with Lack's hypothesis (Moreau 1947, Skutch 1949, Wagner 1957). It is perhaps fitting, therefore, that 63 out of 80 brood manipulation experiments (79%) have failed to support Lack's hypothesis (Table 1.1).

The cost of reproduction hypothesis was embraced by many theoretical life-history ecologists a logical solution to this paradox (e.g., Gadgil and Bossert 1970, Charnov and Krebs 1974, Schaffer 1974). But perhaps the real endearing (and enduring) quality of the cost hypothesis is not so much its ability to explain clutch-size variation in birds, but the extreme difficulty of subjecting the hypothesis to critical testing (Nur 1988*b*). Nevertheless, several long-term studies of individually-marked birds have made much recent headway in determining lifetime reproductive success among individuals (e.g., Clutton-Brock 1988, Newton 1989, Stacey and Koenig 1990). However, in virtually all observational studies, individuals with greater annual reproductive success also survived better than individuals with lower annual reproductive success (Högstedt 1981; Smith 1981, 1988; Fitzpatrick and Woolfenden 1988; McCleery and Perrins 1988; van Noordwijk and van Balen 1988). These studies can all be criticized for not experimentally manipulating levels of parental investment (e.g., Reznick 1985, Nur 1988*b*). High quality parents (or parents holding high quality territories) might be able to invest more heavily in reproduction and in their own maintenance, and thereby attain greater fledging success and have higher survival prospects than would low quality individuals on low quality territories (e.g., Smith 1981). Although the cost hypothesis has had one notable success in explaining

Table 1.1 Brood size manipulation experiments: does observed brood size equal the most productive brood size?

YES: 17 studies[a].

Species	n[b]	Brood size Ctrl	Brood size Expt	Fledglings Ctrl	Fledglings Expt	Source
Diomedea immutabilis	18	1	2	0.67	0.16	Rice & Kenyon 1962
Puffinus tenuirostris	20	1	2	0.70	0.60	Norman & Gottisch 1969
Puffinus puffinus	9	1	2	0.95	0.44	Harris 1966
Pelecanus erythrorhynchus	20	2	3	0.7	0.6	Cash & Evans 1986
Phalacrocorax pelagicus	19	4	5-7	3.60	3.32	Robertson 1971[c]
Calidris pusilla	12	4	5	1.47	0.92	Safriel 1975
Cerorhinca monocerata	13	1	2	0.72	0.62	Summers 1970[c]
Fratercula arctica	10	1	2	0.60	0.50	Nettleship 1972
" "	7	1	2	0.80	0.72	Birkhead & Harris 1985
Aegolius funereus	11	5.9	7.2	4.5	4.0	Korpimaki 1988 (1 year)
Collocalia esculenta	22	1,2	3	1.14	1.00	Bryant & Tatner 1990 (1 year)
Apus apus	16	1.92	4	1.79	1.75	Perrins 1964
Merops viridis	13	<3.9	3-5	1.75	1.42	Bryant & Tatner 1990
Ficedula hypoleuca	24	5.1	9	2.87	2.46	Askenmo 1977
Passer domesticus	14	4.25	5.28	4.25	3.58	Schifferli 1978
Pyrrhula pyrrhula	4	4,5	6,7	4.5	3.75	Newton, *in* Lack 1966
Pica pica	28	5-8	6-9	3.06	0.86	Hogstedt 1980

NO: 63 studies[a].

Species	n[b]	Brood size Ctrl	Brood size Expt	Fledglings Ctrl	Fledglings Expt	Source
Eudyptula minor	10	2	3	0.50	0.69	Daan 1988
Oceanodroma castro	12	1	2	0.50	1.00	Harris 1969
Oceanodroma leucorrhoa	2	1	2	<1.0	1.0	Huntington 1963[c]
Sula bassana	13	1	2	0.94	1.66	Nelson 1964, 1966
" "	30	1	2	0.92	1.84	Wanless 1984[c]
Sula capensis	54	1	2	0.97	1.45	Jarvis 1974
Phalacrocorax auritus	41	4	5-8	3.84	5.08	Robertson 1971[c]
Branta canadensis	159	5.7	.	.	.	Lessells 1986[d]
Anas discors	12	9.7	15.9	5.3	9.5	Rohwer 1985
Necrosyrtes monachus	10	1	2	0.48	0.60	Mundy & Cook 1975
Aquila verreauxii	2	1	2	≤1.0	1.5	Gargett 1970[e]
Buteogallus meridionalis	10	1	2	0.7	1.0	Mader 1982
Rostrhamus sociabilis	12	1-3	3,4	<2.0	2.2	Beissinger 1990
Falco tinnunculus	25	5.0	7.2	4.9	5.7	Dijkstra et al. 1990
Stercorarius longicaudus	4	2	3	1.56	2.49	Andersson 1976
Larus argentatus	49	1-3	4,5	0.92	2.56	Haymes & Morris 1977
Larus fuscus	10	3	4-6	≤3.0	5.00	Harris & Plumb 1965
Larus californicus	22	1,2	3	0.45	0.85	Winkler 1985
Larus glaucescens	97	3	4-6	2.10	3.36	Vermeer 1963[c]
" "	210	3	4-6	2.34	3.50	Ward 1973[c]
" "	79	3	7	2.05	3.29	Reid 1988[f]

Table 1.1: "NO" studies continued next page.

Table 1.1: "NO" studies continued from previous page.

Species	n^b	Brood size		Fledglings		Source
		Ctrl	Expt	Ctrl	Expt	
Rissa tridactyla	4	1-3	4	<3.0	4.00	Coulson, in Lack 1966
" "	3	1-3	4	1.22	2.67	Barrett and Runde 1980[g]
Creagus furcatus	30	1	2	0.56	1.02	Harris 1970
Alca torda	12	1	2	<1.0	1.16	Plumb 1965
" "	14	1	2	0.94	1.14	Lloyd 1977
Cepphus grylle	16	1,2	2,3	0.83	2.06	Asbirk 1979[c]
" "	14	2	3	1.70	2.37	Petersen 1981[c]
Cepphus columba	17	2	3	1.72	1.95	Koelink 1972[c]
Fratercula arctica	4	1	2	<1.0	1.50	Corkhill 1973
Fratercula corniculata	28	1	2	0.91	1.50	Wehle 1983
Columba palumbus	33	2	3	1.96	2.52	Murton et al. 1974
Zenaida macroura	49	2	3	0.60	0.78	Westmoreland & Best 1987
" "	68	2	3	1.08	1.71	Blockstein 1989
Aegolius funereus	8	5.7	6.9	5.0	6.0	Korpimaki 1988 (1 year)
Collocalia esculenta	12	2	3	1.03	1.08	Bryant & Tatner 1990 (1 year)
Collocalia spodiopygius	27	1.9	3	0.92	1.09	Tarburton 1987[h]
Tyrannus tyrannus	2	3.3	5	3.1	5.0	Murphy 1983
Empidonax minimus	7	3-5	5	3.19	4.71	Briskie & Sealy 1989
Tachycineta bicolor	21	5-7	7-9	5.96	7.61	DeSteven 1980
" "	8	5.7	7.9	5.3	7.3	Wiggins 1990
Delichon urbica	5	2.9	5.4	2.5	5.4	Bryant 1975[g]
" "	16	.	6,7	.	5.94	Bryant & Westerterp 1983
Troglodyges aedon	47	6.70	7.79	5.52	6.02	Finke et al. 1987
Turdus pilaris	89	5.12	7.00	4.80	5.83	Slagsvold 1982
Ficedula hypoleuca	.	.	.	.	.	von Haartman 1954[i]
Ficedula albicollis	62	6.0	8.0	5.3	6.0	Gustafsson & Sutherland 1988[g]
Parus montanus	20	7.85	10.14	6.74	7.60	Orell & Koivula 1988
Parus major	250	8.53	11.79	0.43	0.60	Boyce and Perrins 1987[g,j]
" "	55	8.9	13.6	7.9	9.7	Smith et al. 1989
" "	50	7.54	10.98	6.28	7.40	Tinbergen 1987[g]
Parus caeruleus	85	9	12,15	0.91	1.20	Nur 1984b[k]
" "	5	6.4	10	6.4	10	Blondel et al. 1987
Plectrophenax nivalis	11	4	7,8	3.9	6.3	Hussell 1972
Junco phaeonotus } Carpodacus mexicanus}	8	2(3)	4(5)	.	3.0	Wagner 1957[l]
Agelaius phoeniceus	17	2.6	5,6	2.3	3.9	Cronmiller & Thompson 1980
Quelea quelea	6	3	4,5	2.8	2.8	Ward 1965[m]
Passer domesticus	8	3.7	6.3	3.5	5.7	Hegner & Wingfield 1987
Sturnus vulgaris	.	.	.	.	.	Crossner 1977[d]
" "	12	4.48	7	.	6.67	Wright & Cuthill 1990
Sturnus cineraeus	.	.	.	.	.	Kuroda 1959[i]
Corvus frugilegus	18	1.9	4.0	1.9	3.3	Roskaft 1985
Corvus corone	2	4.48	6.48	3.23	3.69	Loman 1980[n]

Notes: taxonomic order follows Howard & Moore 1984 (Basel sequence). I am indebted to Lessells 1986, Ydenberg & Bertram 1989, and Dijkstra et al. 1990 for many of these references.

Table 1.1 footnotes, next page.

Table 1.1 footnotes concluded.

[a] Classification as "yes" or "no" based on point estimates of fledging success. Not all of these "differences" represented singificant differences between experimental and control broods.

[b] Sample size of experimentally enlarged broods; controls almost invariably had much larger samples.

[c] Original not seen; data from Ydenberg & Bertram 1989.

[d] Brood size randomized among birds; fledging success was highest among larger than average broods.

[e] CS = 2, but 2nd-hatched young invariably killed by 1st-hatched young (reviewed in Simmons 1988). Investigator experimentally raised one chick in captivity and added it to nest after period of intense siblicidal attacks was over.

[f] Other experimental brood sizes also created, data are for the largest experimental BS.

[g] Values visually estimated from figures.

[h] Control fledging success is for broods of two; fledging success from natural broods of one is much lower and would further increase the disparity in fledging success between enlarged and normal broods.

[i] Original not seen; referenced in Dijkstra et al. 1990.

[j] Number of offspring recruited into breeding population.

[k] Survival measured at 3 months post-fledging.

[l] Pooled data, cannot separate by species.

[m] Enlarged broods not different from control broods of 3, but approximately 25% of natural broods are of 2, so enlarged broods fledge more than population mean.

[n] Recalculated, direct figures not presented in the original paper.

clutch size under conditions of experimentally manipulated brood sizes (Gustafsson and Sutherland 1988), many other studies have either failed to demonstrate reproductive costs, or the costs in these studies have not been sufficient to offset the increases in fledging success (e.g., DeSteven 1980; Nur 1984*a*, 1988*a*; Boyce and Perrins 1987; Hegner and Wingfield 1987; Reid 1987; Korpimäki 1988; Pettifor *et al.* 1988; Wiggins 1990; but see Nur 1988*b*, Daan *et al.* 1990 for a more optimistic view of the cost hypothesis).

These difficulties have led many researchers to reconsider egg formation costs as an important limiting factor on clutch size. Although Lack rather quickly dismissed this hypothesis in his earlier writings (Lack 1947*a*, 1954), he came gradually to accept egg formation costs as an important factor affecting both clutch size and timing of breeding (Lack 1956, 1964, 1966, 1967, 1968). The most convincing case histories for this hypothesis involve arctic-nesting geese (Ryder 1970, Ankney and MacInnes 1978, Raveling 1979, Ankney 1984). These species arrive on their arctic breeding grounds before food is generally available, and they produce eggs by using fat and protein that they stored in their bodies ("endogenous nutrient reserves") during migration to the breeding grounds (Ankney and MacInnes 1978, Alisauskas 1988). In this relatively "simple" system, there is good evidence from at least one species that the size of a female's nutrient reserve influences the size of clutch that she can lay and incubate successfully (Ankney and MacInnes 1978). Egg formation costs have since been implicated for a variety of temperate- and tropical-nesting species of birds (reviewed by Drent and Daan 1980, Winkler and Walters 1983, Murphy and Haukioja 1986, Ankney and Alisauskas *in press*), but there is a very important distinction between arctic geese and other birds. Arctic geese are absolutely dependent on reserves (Ryder 1970, Ankney and MacInnes 1978), whereas most temperate and tropical birds can obtain nutrients for egg production directly from their diets.

There is also an important conceptual difference between the egg formation hypothesis and Lack's brood-provisioning hypothesis. Lack's hypothesis implied that clutch size was ultimately regulated by average food availability during the brood-rearing period, hence parents would not be expected to respond proximately to variations in food supply. Furthermore, clutch size would not have to be optimal during all years, only on average. However, he egg formation hypothesis implies that clutch size is proximately constrained by food availability during the egg laying period, and hence this hypothesis can be tested directly by examining variation in clutch size with respect to food availability (Daan *et al.* 1988). Furthermore, the egg formation hypothesis implies that birds should lay as many eggs as they possibly can (subject to fitness constraints imposed by trade-offs with other essential activities).

Alisauskas and Ankney (1985) have implied that clutch size in the American Coot (*Fulica americana*) is limited by the ability of females to produce eggs, and this is the species and topic that I selected to conduct my doctoral research on. My general question was: "Is clutch size in the American Coot limited by the ability of females to produce eggs?"

1.2 SCOPE OF THESIS

This thesis is organized into six chapters. The first (and present) chapter outlines the conceptual problem addressed herein, as well as providing a brief historical sketch of the principal ideas. The second chapter provides background information on the study organism and the study area, and is intended primarily for readers who are unfamiliar with coots and prairie wetlands. Chapter 2 also describes supplemental-feeding methods that are relevant to all ensuing chapters. The next three chapters present observational and experimental research designed to test the egg formation hypothesis in American Coots; these chapter divisions represent intended publication units. Chapter 3 examines variation in laying date, clutch size, and egg size; Chapter 4 assesses patterns of variation in the nutrient content of eggs; and Chapter 5 examines nutrient reserve dynamics of adults during the breeding season. In the sixth and final chapter, I review current hypotheses of food limitation for breeding American Coots, and I attempt to provide some alternative explanations for observed patterns of clutch-size variation. The thesis also includes six appendices; these include nutritional information on supplemental foods (Appendix 1), justification for specific techniques employed in other analyses (2, 3, 5, and 6), or data too unwieldy for conventional presentation in tables or figures (4).

CHAPTER 2. STUDY ORGANISM, STUDY AREA AND SUPPLEMENTAL FEEDING PROCEDURES

2.1 STUDY ORGANISM

The American Coot (*Fulica americana*; order Gruiformes, family Rallidae; hereafter "coot") is an abundant and conspicuous component of North America's wetland avifauna (Kantrud and Stewart 1984). Their breeding range encompasses most of the southern two-thirds of the continent, with their northern range being approximately delimited by the southern edge of the boreal zone (National Geographic Society 1987). Although their breeding range is vast, the majority of coots breed in the Prairie Pothole Region of south-central Canada and the north-central U.S. During the 1988 and 1989 aerial waterfowl surveys (conducted jointly by the U.S. Fish & Wildlife Service and the Canadian Wildlife Service), 45 and 52% of the surveyed coots occurred in the southern Canadian prairies (the surveyed area includes most of Alberta, Saskatchewan, Manitoba, North Dakota, South Dakota, and Montana, as well as portions of western Ontario, Northwest Territories, Yukon Territory, and Alaska) (Didiuk and Caswell 1989). American Coots are migratory in the northern portions of their range (including all of the Prairie Pothole Region), but may be sedentary in the south (Gullion 1953).

Coots are renowned for their capacity to pioneer new habitats (Weller and Fredrickson 1974). To some extent, the Prairie Pothole population is panmictic, with coots redistributing themselves each spring in response to geographic variation in wetland conditions (Fig. 2.1). Consequently, there is no recognized subspecific variation in North American populations of the American Coot (Howard and Moore 1984), although Alisauskas (1987) presented evidence of clinal variation in culmen (bill) length. This is in marked contrast to the situation in Central and South America, where geographic isolation of wetland habitats and the resulting sedentary habits of the wetland avifauna (Fjeldså 1985) have produced nine species and/or subspecies of *Fulica* (Howard and Moore 1984).

American Coots are primarily herbivorous, feeding on submerged aquatic

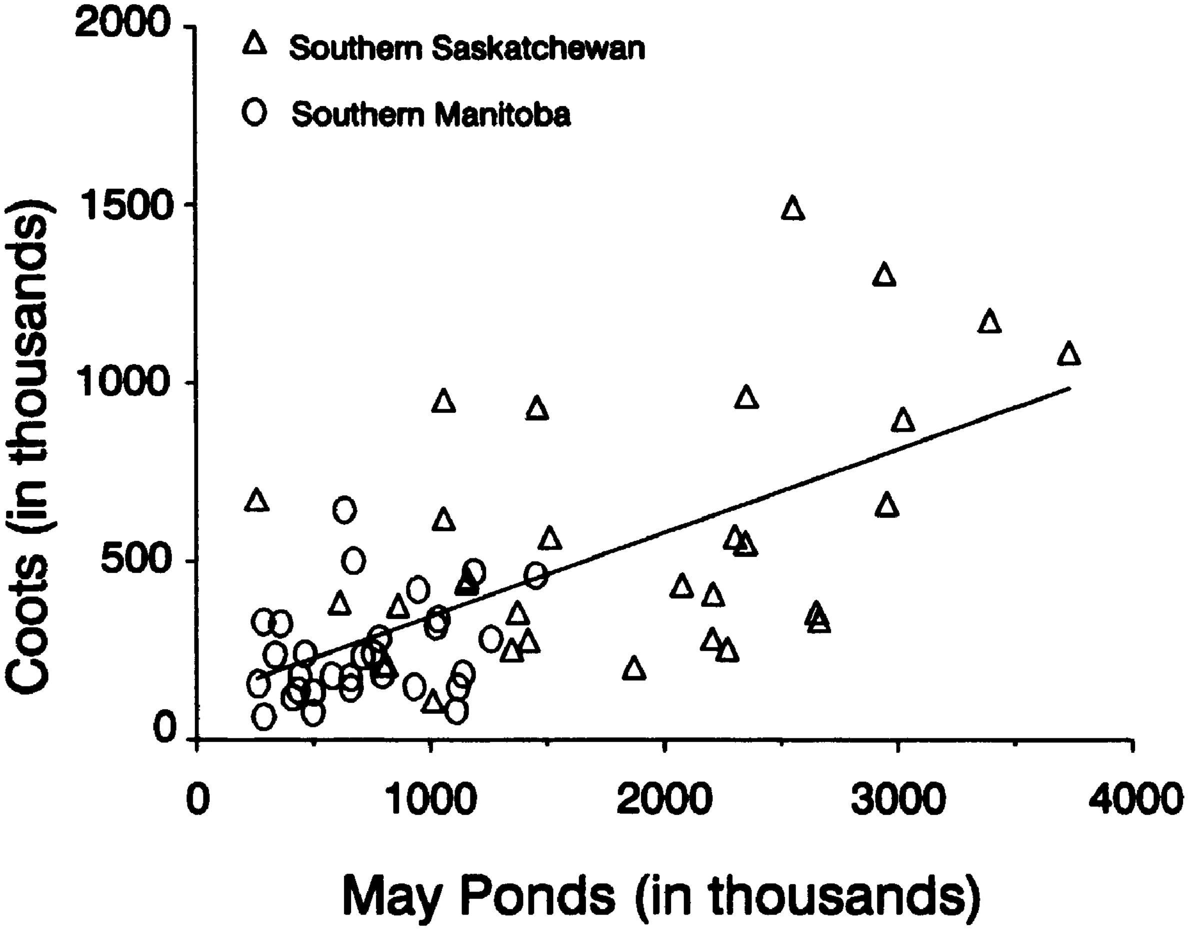

Fig. 2.1. Relationship between numbers of breeding American Coots and numbers of wetlands, as determined from annual aerial surveys by the U.S. Fish & Wildlife Service and the Canadian Wildife Service. Data are from 1961 - 1990; each point represents a different year. The relationship is highly significant (P < 0.0001).

vegetation, seeds (of emergents, submergents, and mudflat annuals), and algae (Jones 1940, Sooter 1941, Stollberg 1949, Colbo 1965, Fitzner *et al.* 1980). In some studies, aquatic invertebrates have comprised a substantial (e.g., 45 to 85%) proportion of the diet in young chicks (Jones 1940, Sooter 1941, Driver 1988; but see Fitzner *et al.* 1980, Eichhorst 1986). In general, however, coot diets have been rather poorly documented (Driver 1988 is a notable exception) due to problems associated with rapid throughput, post-mortem digestion, and differential retention of food items in the gizzard (Swanson and Bartonek 1970; Eichhorst 1986; Arnold, *pers. obs.*).

In prairie Canada, coots generally return from the wintering grounds during mid- to late-April, with males and older birds generally arriving before females and younger birds, respectively (Ryan and Dinsmore 1979, Alisauskas and Ankney 1985). Like other small-bodied slow-flying birds, they migrate exclusively at night, presumably as an evolutionary response to predation by diurnal raptors. Previous researchers have not agreed on whether courtship and pairing occurs before or after migration and territory establishment (Sooter 1941, Gullion 1953, Ryan and Dinsmore 1979, 1980, Alisauskas and Ankney 1985; see also Cavé *et al.* 1989). Part of this difficulty is undoubtedly related to the inability of investigators to determine sex of coots by external visual examination (Eddleman and Knopf 1985). Coots defend their territories vigorously against conspecifics, as well as other species of wetland birds (Ryder 1959). Territories are used exclusively for all activities from prelaying through brood-rearing (Gullion 1953).

Coots construct floating nests of dead vegetation which are concealed in emergent vegetation, usually in residual cover from the previous year. They produce a maximum of one brood per year in the northern part of their range, but farther south they may exhibit clutch-brood overlap (Iowa: Fredrickson 1969, Wisconsin: Bett 1983, Washington: Hill 1986) or raise two sequential broods per year (California: Gullion 1954). They are persistent renesters throughout their range (i.e., producing a replacement clutch following the destruction of an earlier nesting attempt) (Hill 1984, 1989; Sutherland 1984; this study), with individual females producing up to five sequential clutches in response to repeated nest failures (this study). Both sexes participate in territory defense, nest construction, incubation, and brood-rearing, although there are some sexual differences in activity budgets with respect to these behaviors (Ryan and Dinsmore 1979). Some individuals are intraspecific brood parasites, laying their eggs in other (host) coots' nests and thereby exploiting the parental care of the hosts (Sooter 1941; Fredrickson 1970; Lyon, *in press*; Arnold, *unpubl. data*).

Coots have large and exceptionally variable clutches (Table 2.1), making them particularly well-suited for research on the causes and consequences of clutch-size variation. Coefficients of variation for clutch size in 3 coot populations equaled or exceeded clutch size CV's for 21 other species selected systematically from studies in my Literature Cited (Table 2.1). It is not known how much of this variation is heritable, but studies of clutch-size heritability in other species of birds suggest that it could be anywhere from 0 to 50% (Gibbs 1988, van Noordwijk and van Balen 1988). Coot eggs are fairly nutrient-rich (Alisauskas 1986) and are typically produced at the rate of one egg per day (Sooter 1941; this study). Inter-individual variation in egg size is not as extreme as for clutch size, but compared to most other birds, coots have fairly variable eggs (Table 2.1; some passerines have more variable eggs). Alisauskas and Ankney (1985) suggested that approximately 85% of the lipid and 28% of the protein used in clutch formation were obtained from endogenous (carcass) reserves acquired before arrival on the breeding grounds, thus implying that 15% of the lipid and 72% of the protein were obtained directly from the diet during the egg-laying period (i.e., exogenously). If coots rely on endogenous reserves for clutch formation, and if these reserves are limited by physiological constraints and/or by food availability prior to breeding, then these reserves might also limit clutch size, as has been suggested for several species of waterfowl (reviewed in Chapter 5).

Incubation capacity has generally only been invoked as a limitation to clutch size among species having sharply truncated clutch-size distributions (e.g., gulls, shorebirds), which certainly rules out coots (see Fig. 3.1); furthermore,

Table 2.1. Clutch- and egg-size variation in *Fulica americana* and other birds.

	Clutch size			Egg size[a]			
Species	X	SD	CV	X	SD	CV	References
Fulica americana	7.2	2.0	28	28.9	1.9	7	1, 2
	6.3	2.0	32	27.4	2.5	9	3
	8.1	1.9	23	28.3	2.5	9	4
Podilymbus podiceps	7.3	1.3	18	21.6	1.4	6	5, 6
Puffinus puffinus	1.0	0.0	0	51.1	4.0	8	7
Chen caerulescens	4.0	0.8	20	121.0	7.0	6	8, 9
Anas acuta	6.9	1.5	22	37.5	2.6	7	10, 11
Anas discors	10.4	1.4	13	28.1	2.5	9	12, 13
Calidris minutilla	3.9	0.3	9	6.5	0.3	5	14
Tringa nebularia	3.8	0.2	5	30.9	2.1	7	15
Larus argentatus	2.8	0.4	16	98.0	8.0	8	16
Fratercula arctica	1.0	0.0	0	70.4	5.6	8	17
Aegolius funereus	5.9	0.8	14	11.8	.	3	18
Apus apus	2.2	0.5	21	3.4	0.2	5	19, 20
Empidonax minimus	3.9	0.5	12	1.5	0.2	11	21, 22
Delichon urbica	3.6	0.8	23	1.7	0.2	14	23
Corvus corone cornix	4.3	0.7	16	19.4	2.2	11	24
Pica pica	6.5	1.1	17	8.7	0.8	9	25
Parus major	9.5	1.1	12	1.6	0.1	5	26, 27
Ficedula hypoleuca	6.4	0.9	14	1.6	0.1	7	28
Oenanthe oenanthe	6.2	0.7	11	2.7	0.3	10	29
Sturnus vulgaris	5.1	1.1	21	6.9	0.3	4	30, 31
Sturnella neglecta	5.4	0.9	17	5.2	0.5	9	32
Quiscalus major	2.6	0.5	19	8.1	0.9	11	33

Notes: CV's calculated prior to rounding. References on following page.

References for Table 2.1: 1, Alisauskas & Ankney 1985; 2, Alisauskas 1986; 3, Bett 1983; 4, B. E. Lyon, *pers. comm.*; 5, Arnold 1989; 6, Arnold 1990; 7, Brooke 1978; 8, Ankney & Bisset 1976; 9, Ankney 1980; 10, Duncan 1987*a*; 11, Duncan 1987*b*; 12, Rohwer 1985; 13, Rohwer 1986*a*; 14, Miller 1979; 15, Thompson *et al.* 1986; 16, Meathrel *et al.* 1987; 17, Birkhead & Nettleship 1984; 18, Korpimäki 1989: Egg size CV for length only; 19, Lack & Lack 1951; 20, O'Connor 1979; 21, Briskie & Sealy 1989; 22, Briskie & Sealy 1990; 23, Bryant 1978; 24, Loman 1984; 25, Hochachka & Boag 1987; 26, Smith *et al.* 1989; 27, Ojanen 1983; 28, Jarvinen & Väisänen 1983; 29, Moreno 1989*b*; 30, Lack 1948*a*; 31, Greig-Smith *et al.* 1987; 32, Dickinson *et al.* 1987; 33, Bancroft 1984.

Fredrickson (1969) has shown experimentally that coots can incubate clutches of up to 21 (more than double the mean) with no loss in hatching success.

Coots begin incubation before their clutch is complete, which results in asynchronous hatching among brood-mates (hatch may be spread over a week or more). Hatchling coots are semi-precocial (Precocial IV; Nice 1962); they can leave the nest within hours of hatching, but they are critically dependent upon their parents for food (and warmth) for at least the first 10 days after hatching (Ryan and Dinsmore 1979, Desroschers and Ankney 1986, Driver 1988; see also Horsfall 1984*a*,*b*), suggesting that the ability of parents to provision young chicks may limit clutch size, as suggested by Lack (1947*a*) for a variety of altricial and semi-precocial birds. Coots rapidly gain proficiency at foraging for themselves (Desroschers and Ankney 1986, Driver 1988), and become increasingly less dependent on their parents for food. Many coot broods are deserted by their parents before they have fledged (attained flight capability) at about 50 - 60 days of age (Ryan and Dinsmore 1979; Arnold, *pers. obs.*).

In late summer, the adults undergo a simultaneous wing molt, which renders them flightless. Brood abandonment may be a consequence of the benefits that accrue to coots by migrating to large, stable water-bodies before going flightless (Hohman et al., *in press*). However, many adults initiate the wing molt on the breeding ponds (C. D. Ankney and T. W. Arnold, *unpubl. data*). In late summer, nearly all adult coots depart from smaller breeding potholes and concentrate on large staging areas (e.g., Lake Winnibegosis, Manitoba) in preparation for fall migration (Arnold, *pers. obs.*).

2.2 STUDY AREA

I studied coots at the Minnedosa Substation of the Delta Waterfowl & Wetlands Research Station, located in southwestern Manitoba approximately 10 km SE of the town of Minnedosa (50°16'N, 99°50'W). The Minnedosa study area was comprised of numerous small (0.1 -3.0 ha) palustrine persistent emergent wetlands (wetland classification follows Cowardin *et al.* 1979) that ranged from seasonally-flooded (ponds normally dry up by late summer) to semipermanently-flooded (water persists in most years) to intermittently-exposed (i.e., 'permanent;' water persists in all but extreme drought years). Wetlands were classified into the previous categories based on physiognomy and species composition of the vegetation (Stewart and Kantrud 1971, Cowardin *et al.* 1979); seasonal wetlands were dominated by whitetop (*Scholochloa festucacea*) and sedges (*Carex* spp.), semipermanent wetlands by cattails (*Typha angustifolia* and *T. latifolia*), and permanent wetlands by hardstem bullrush (*Scirpus acutus*). Of 68 wetlands comprising my roadside transect survey (described below), 17% were seasonal, 78% were semipermanent, and 6% were permanent. During drought conditions, many wetland basins were dominated by Dock (*Rumex mexicanus*) and smartweeds (*Polygonum* spp.). Submerged aquatic beds comprised of pondweeds (*Potamogeton* spp., especially *P. pectinatus*), water milfoils (*Myriophyllum* spp.), and coontails (*Ceratophyllum* spp.) dominated the deep-water portion of most semipermanent and permanent wetlands.

Prairie wetlands exhibit pronounced annual variation in early-spring water levels, primarily due to fluctuations in evaporation and rainfall the previous summer, and in snow accumulation during the preceding winter (Stoudt 1982). Water-level variation can strongly affect the productivity of wetlands, and hence their attractiveness and value to breeding waterbirds (Weller and Fredrickson 1974). At Minnedosa, water levels varied widely in response to annual and/or seasonal trends in precipitation (Fig. 2.2). May wetland conditions (which may affect settlement and reproductive decisions of coots) were described as fairly wet in 1986 and 1987, average in 1988, very dry in 1985 and 1990, and extremely dry in 1989 (Fig. 2.2, Table 2.2). These assessments of relative water-levels are based on long-term (i.e., 30 year) patterns of variation, not just the years in question; 1983 was the last very wet spring in southern Manitoba.

July water conditions (which likely affect fledging success) were described as fairly wet in 1986 and 1987, fairly dry in 1985 and 1988, very dry in 1990, and extremely dry in 1989 (Fig. 2.2). By late August in 1989, most wetlands on my roadside survey route were completely dry.

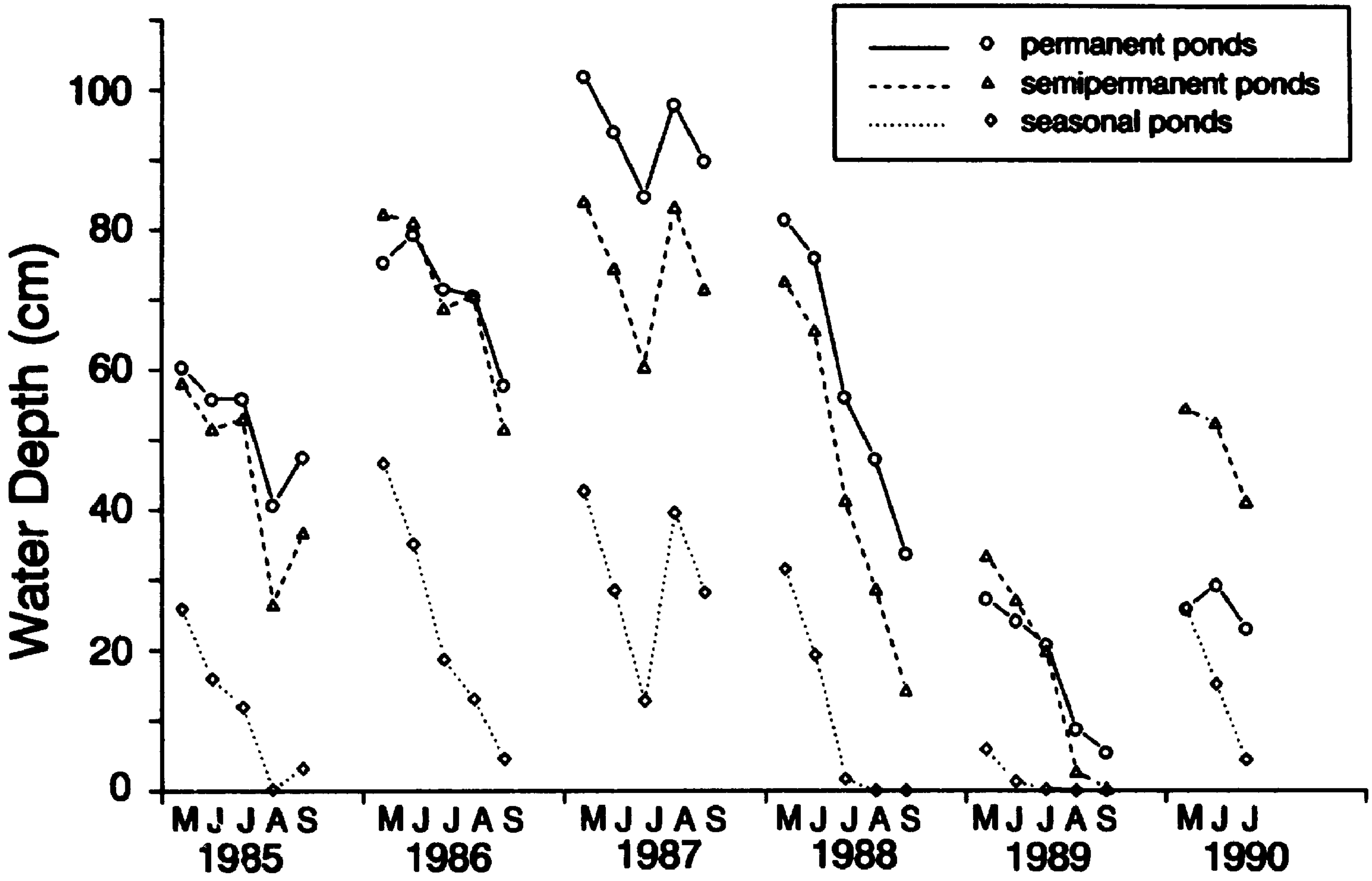

Fig. 2.2. Annual and seasonal variation in wetland water depths on the Minnedosa Study Area. Each data point represents the sample mean form 8 permanent, 12 semipermanent, or 16 seasonal wetland basins. The same wetlands were sampled at the same exact location during the middle of each month.

Table 2.2. Annual variation in wetland conditions, arrival chronology (Julian dates), and population density of American Coots on the Minnedosa Study Area (MDSA) and in southern Manitoba (S Man.).

Year:	May Water Depth (cm) MDSA	May Ponds (1000's) S Man.	Earliest Arrival Date MDSA	Peak Arrival Date MDSA	Peak Numbers MDSA	May Count (1000's) S Man.
1985	58.08	496.3	105	--	--	75.0
1986	82.28	947.6	105	--	--	421.7
1987	84.08	498.4	105	119	210	133.0
1988	72.61	632.5	99	124	322	644.3
1989	33.47	286.5	109	129	42	63.9
1990	54.42	658.6	109	133	130	145.3

Notes: MDSA = Minnedosa Study Area, S Man. = southern Manitoba, Strata 36 - 40, U.S.F.W.S. and C.W.S. air-ground waterfowl surveys. May water depth is from Fig. 2.2 (data from M. G. Anderson and R. Emery, pers. comm.), earliest arrivals are from unpubl. arrival records (Delta Waterfowl & Wetlands Research Station, MDSA), peak arrivals and numbers are from roadside transects (Fig. 2.3; Arnold, unpubl. data), and S. Man. May ponds and coot numbers are from the Canadian Wildlife Service (A. B. Didiuk, F. D. Caswell, and G. S. Hochbaum, unpubl. reports).

Arrival of migrant coots at Minnedosa peaked on 29 April in 1987, and was progressively later in succeeding years (Table 2.2, Fig. 2.3; data were unavailable for 1985 and 1986). Breeding coot densities were very high in 1986 and 1988, fairly high in 1987, fairly low in 1985 and 1990, and extremely low in 1989 (Table 2.2 and Arnold, *pers. obs.*). In 1987, my study area encompassed about 16 km^2 and included approximately 62 wetlands (not all wetlands on the study block were included). In 1988, I expanded the study area to about 23 km^2 and 121 wetlands. In 1989, the severe drought year, my study area included all wetlands in an approximately 75 km^2 area that were known or thought to have breeding coots (51 wetlands included, only 21 of which eventually had nesting activity).

2.3 SUPPLEMENTAL FEEDING PROCEDURES

Supplemental feeding experiments were conducted from 1987 through 1989. In 1987, steam-rolled corn and trout chow were provided independently in a 2 x 2 factorial design (± corn, ± trout chow). Corn contains approximately 80% nitrogen-free extract (NFE), and is an excellent diet for lipogenesis (Alisauskas *et al.* 1988). Trout chow (Martins 84G, Martin Feed Mills, Elmira, Ontario) contains > 40% crude protein, and includes a full complement of amino acids. Supplemental food was placed on floating platforms located within the territories of breeding coot pairs. Because I did not want supplemental food to influence settling patterns (i.e., high-quality birds selecting areas with feeders), I did not provide food until after the peak of spring arrival and territory establishment (as determined by regular roadside surveys of 68 wetlands; Fig. 2.3). Feeding began on 27 April 1987, 17 days before the mean date of nest initiation (initial clutches only), and continued until no newly initiated nests were found. Platforms were refilled every 4 days with approximately 0.5 kg of food. In order to prevent food piracy among neighboring coot pairs, all pairs on a wetland received the same food supplement (i.e., food supplements were randomly assigned to wetlands, rather than coot pairs). Approximately 400 kg of

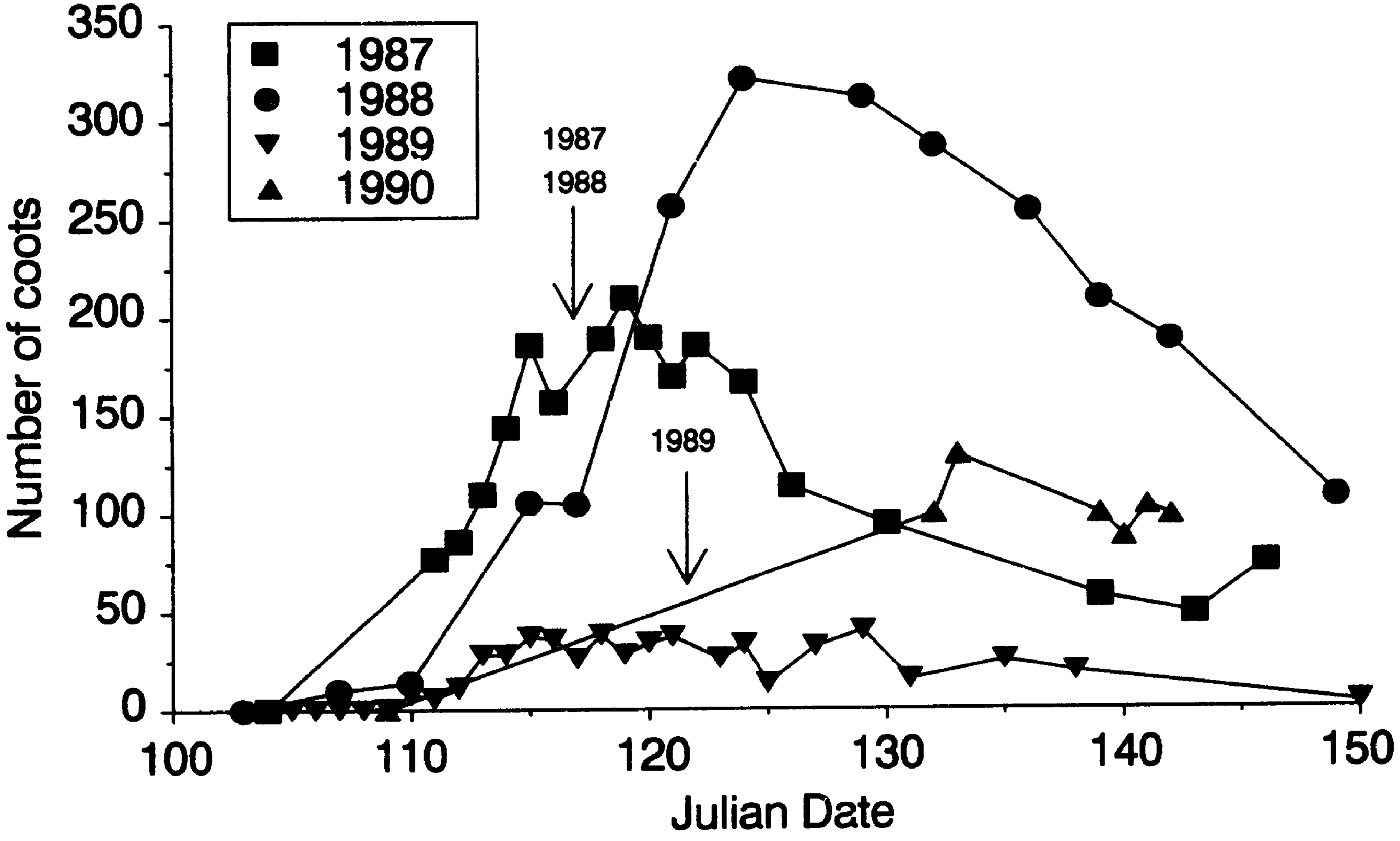

Fig. 2.3. Annual and seasonal variation in numbers of American Coots on the Minnedosa Study Area, based on a standard roadside survey. Apparent declines after day 120 during 1987 and 1988 reflect declining visibility due to onset of nesting activity, rather than true declines in numbers. Arrows indicate initiation of supplemental feeding in 1987-89.

supplemental food were dispensed in 1987.

In 1988 and 1989, only one food supplement was provided; fed birds received a mixture of steam-rolled corn, rabbit chow, layer diet, oystershell, and grit in an approximate 20:10:10:1:1 ratio. Rabbit chow (Bunny Booster, Cargill Ltd., Winnipeg, Manitoba) contained > 18% crude protein. I replaced trout chow with rabbit chow because coots seemed reluctant to eat trout chow, and I was uncertain if this was due to low palatability or to lack of demand for protein. But because coots are primarily herbivorous, I reasoned that they may be more attracted to a high protein diet consisting entirely of plant proteins. The layer diet (Co-op Layer Diet 20, Federated Co-operatives Ltd., Saskatoon, Saskatchewan) was a complete diet especially formulated for egg production in domestic chickens, and it therefore provided all essential nutrients for egg formation (≥ 18% crude protein, ≥ 3% crude fat, and 3.06% calcium). In 1988, the layer diet was replaced with a chick diet (Co-op Chick Starter - 18%, Federated Co-operatives Ltd.) when the first chicks started hatching (approximately 10 June). I also provided oystershell as an additional calcium supplement, and medium poultry grit to assist in mechanical breakdown of supplemental and/or natural foods (especially corn) in the gizzard. Feeding began on 27 April 1988 and 2 May 1989, 22 and 14 days before the mean dates of nest initiation, respectively. In 1988, feeding continued until late June on most of the study area, but was extended until early August on wetlands where I monitored brood-rearing activities. In 1989, feeding continued until no new nests were discovered. Food was provided similarly to 1987, except that platforms were refilled every third day. In 1988, I provided approximately 2700 kg of food supplements, and in 1989 approximately 500 kg. Nutritional content of supplemental foods is presented in Appendix 1. Coots were observed feeding from platforms on numerous occasions each year, but no quantitative data were obtained on frequency of platform use.

CHAPTER 3. PATTERNS OF VARIATION IN LAYING DATE, CLUTCH SIZE, AND EGG SIZE

3.1 INTRODUCTION

Birds normally initiate nesting only at certain times of the year (Lack 1950*a*, Barry 1962). Among arctic-nesting species, this specificity in breeding times can be explained by the relatively short period of amenable weather; birds have to initiate breeding soon after spring thaw in order to complete their reproductive cycle before fall freeze-up (Cooch 1961, Barry 1962, Lyon and Montgomerie 1987). Temperate- and tropical-nesting species should be less constrained by severe weather conditions, yet most of these species also exhibit seasonal peaks of reproduction (Lack 1950*a*,*b*; Moreau 1950; Skutch 1950). Lack (1933, 1947*a*, 1950*a*, 1954) proposed that nesting seasons had evolved so that food availability was at its seasonal maximum when parents were feeding nestlings. Birds nesting much earlier or later than the population mean would therefore leave fewer surviving offspring. But because birds initiate egg-laying two or more weeks before their eggs hatch, and because it seemed unlikely that food availability could remain unchanged for such a long period, Lack proposed that timing of breeding was proximately regulated by factors other than food availability (i.e., photoperiod in temperate zones, rainy seasons in tropical zones; Lack 1947*a*, 1954; see also Rowan 1926, Baker 1938). Lack stressed that such external synchronizers were not the ultimate reason why birds bred when they did; these proximate cues were important only so long as they accurately predicted seasonal food abundance.

Lack (1954) recognized that many populations of birds exhibited significant annual variation in timing of breeding, an observation that was seemingly at odds with his hypothesis. Lack reasoned that many birds were able to fine-tune their breeding schedules by reacting to cues that, on average, served as reliable predictors of annual variation in food abundance (e.g., Gibb 1950, Lack 1966, Perrins and McCleery 1989). Cues thought to be important included spring temperatures, vegetation growth, and, in some cases, current food availability (i.e., for several vole-eating raptors, early spring vole densities could reliably predict prey abundance later in the nesting season; Korpimäki 1987).

Lack's hypothesis came under early criticism from one of his own students. Perrins (1965, 1966) showed that the earliest nesting pairs of Great Tits (*Parus major*) and Manx Shearwaters (*Puffinus puffinus*) raised the most offspring, yet the majority of pairs began nesting a week or more after this most productive time. Based on these findings, Perrins (1970) modified Lack's hypthesis to suggest that many birds were prevented from breeding at the optimal time for raising young because they lacked sufficient resources for producing eggs. Thus, the egg formation hypothesis became an important component of Lack's ideas on the timing of breeding in birds (Lack 1966, 1968), just as it had done for clutch size (see Chapter 1). However, as Daan *et al.* (1988) have pointed out, Perrin's hypothesis implies an immediate, as opposed to future, constraint on timing of breeding, hence birds should respond proximately to alterations in food availability by adjusting their timing of breeding.

Hypotheses of clutch size limitation have been reviewed in Chapter 1, and will not be repeated here. As was the case with Lack's timing of breeding hypothesis, annual variation in clutch size was seemingly at odds with Lack's brood-provisioning hypothesis (Lack 1947*a*), unless cues available at the time of egg laying could accurately predict annual variation in food availability during the nestling period (Lack 1947*a*, 1954).

Some of the most ubiquitous patterns of within-population clutch-size variation involve seasonal changes in mean clutch size (Lack 1947*a*, 1954; Daan *et al.* 1988). Lack (1947*a*) described three general patterns of seasonal variation in clutch size: (1) in birds with obligate clutch sizes (i.e., in Procellariformes clutch size is always one; in Columbiformes it is always one or two, depending on species) there is no clutch-size variation of any sort, including seasonal variation (e.g., Brooke 1978, Westmoreland and Best 1987, Blockstein 1989); (2) in birds that produce only one or two broods per season (i.e., most temperate- and arctic-nesting birds), clutch size declines monotonically throughout the breeding season

(Klomp 1970: Table 5 lists 116 references for this pattern), and (3) in some birds which produce two or more broods per season, clutch size increases over the early portion of the season, reaches a plateau in mid-season, and then declines towards the end of the breeding season (Klomp 1970: Table 5 lists 40 references).

Lack (1947*a*, 1954) suggested that seasonal clutch-size declines were ultimately related to declining length of daylight during the summer, and hence the amount of food that parents could bring to nestlings in a normal working day. Clutch size does indeed decline seasonally for species that raise nestlings after the June 21st solstice; but for species that fledge their young before the solstice, while daylength is still increasing, clutch size nevertheless declines with laying date (Klomp 1970: Fig. 3). Likewise, multi-brooded species with initial increases and terminal declines in clutch size exhibit no strong concordance between peak seasonal clutch size and daylength (Klomp 1970: Fig. 4).

Although the correlation between potential foraging time and clutch size is rather poor, this does not necessarily refute the brood-provisioning hypothesis. Seasonal variation in absolute food abundance might be the overriding factor affecting levels of parental food provisioning to nestlings (Lack 1954). Food abundance is understandably much harder to quantify than is daylength, but several studies have nevertheless obtained data on seasonal variation in both food and clutch (or brood) size (Gibb 1950, Dunnet 1955, Gibb and Betts 1962, Mebs 1964, Hussell 1972, Bryant 1975, Murton and Westwood 1977, Murphy 1986*b*, Hussell and Quinney 1987, Korpimäki 1987, Lyon et al. 1987, Daan *et al.* 1988). Collectively, these data show no obvious seasonal patterns. Although all species breed at or near the seasonal peak in food abundance (e.g., Lack 1950*a*), some species breed during the upswing in food abundance, some during the plateau phase, and some during the decline phase (Daan *et al.* 1988). All of these species, however, exhibit seasonally declining clutch size.

Many of the most pronounced seasonal declines in clutch size occur among species of waterfowl (Sowls 1955, Barry 1962, Batt and Prince 1979, Krapu 1981, Birkhead *et al.* 1983, Afton 1984, Toft *et al.* 1984, Hamann *et al.* 1986, Duncan 1987*a*, Rhymer 1988*b*, Hamann and Cooke 1989, Rohwer and Eisenhauer 1989, Lokemoen *et al.* 1990), for which the brood provisioning hypothesis is clearly inappropriate (e.g., Lack 1947*a*, Rohwer 1985, Lessells 1986). Researchers working on waterfowl have typically attributed seasonally declining clutch size either to effects of parental age or to effects of renesting (e.g., Johnsgard 1973). Young waterfowl typically begin nesting later and also produce smaller clutches (e.g., Finney and Cooke 1978, Krapu and Doty 1979; general review in Sæther 1990), hence seasonally declining clutch size is viewed as an artifact of age structure of the nesting population. However, clutch size also declines seasonally within age classes of waterfowl (e.g., Dane 1966, Alliston 1979 [adults exhibit declines, but yearlings do not], Batt and Prince 1978, Gauthier 1989, Hamann and Cooke 1989, Lokemoen *et al.* 1990). Likewise, renesting waterfowl necessarily nest later in the season and invariably produce smaller clutches, on average. Renesting birds are presumed to exhaust their nutrient reserves while laying the first clutch, and hence they cannot produce a large renest clutch (e.g., Sowls 1955, Krapu 1981). However, seasonally declining clutch size has been observed in populations where females do not renest (Barry 1962, Gauthier 1989, Rohwer and Eisenhauer 1989, Hamann and Cooke 1989) and in populations where renesting birds could be identified and excluded from analysis (Alliston 1979, Batt and Prince 1979). Thus, seasonal declines of clutch size among waterfowl cannot be accounted for by hypotheses that pertain only to waterfowl, hence a more parsimonious explanation is needed to explain this phenomenon among birds in general.

Perrins (1970) proposed that food for the laying female might influence both timing of breeding and clutch size. Thus, it would be advantageous for most birds to nest somewhat earlier and produce larger clutches, but many females lack the resources necessary to produce eggs at the optimal time for subsequent brood rearing. Such birds delay nesting in order to acquire more reserves (or to allow exogenous food resources to increase), but delaying nesting means that these individuals will no longer produce nestlings at the optimal time, and hence optimal clutch size declines seasonally. As a result of this seasonal decline in optimal clutch size, there is also a seasonal decline in the minimum threshold of nutrient reserve levels and/or exogenous food abundance necessary for females to initiate nesting (i.e., smaller clutches can be produced with fewer nutrients) (Perrins 1970, Reynolds 1972, Drent and Daan 1980, Birkhead *et al.* 1983).

Nutrient investment in clutch formation is a function of egg size, in addition to clutch size. Egg size (fresh mass and/or volume) varies considerably within species of birds, with a large component of this variation being attributable to additive genetic variance (reviewed in Boag and van Noordwijk 1987, Lessells *et al.* 1989). Highly heritable characters are theoretically presumed to have a low association with fitness (Falconer 1981, Gustafsson 1986); however, egg size has been positively correlated with several likely components of offspring fitness. Some of the potential benefits of large eggs include greater hatchability (O'Connor 1979, Slagsvold *et al.* 1984, Rofstad and Sandvik 1985, Martin and Arnold 1991; but see Briskie and Sealy 1990), larger hatchling size and/or mass (Ricklefs *et al.* 1978, Furness 1983, Alisauskas 1986; numerous additional studies), faster post-hatching growth (Schifferli 1973, Ankney 1980, Furness 1983, Rhymer 1983; but see Ricklefs 1984*a*), greater asymptotic size (Furness 1983, Ricklefs 1984*a*), enhanced thermoregulation (Rhymer 1988*a*), greater fasting endurance (Krapu 1979, Ankney 1980), and greater nestling survival (Parsons 1970, Howe 1976, Nisbet 1978, Lundberg and Väisänen 1979, Furness 1983, Quinn and Morris 1986, Hébert and Barclay 1988, Veiga 1990; but see Barrett and Runde 1980, Bancroft 1984, Arcese and Smith 1988, Ollason and Dunnet 1988).

If egg size is highly heritable, and if egg size can affect the fitness value of offspring, then there must also be certain disadvantages associated with large eggs, otherwise strong directional selection should have acted to eliminate any additive genetic variation in egg size. However, this has clearly not occurred, as most studies have documented rather high levels of intra-population egg-size variation (e.g., Table 2.1).

Lack (1967) hypothesized that food may be limiting for laying female waterfowl, and hence, species producing relatively large eggs (for their body size) would have to compensate by laying relatively few eggs. Lack did not seem to consider that if food was abundant enough to produce a large egg on one day, it should also be abundant enough to produce a large egg the next day (Rohwer 1988). Ryder (1970), however, suggested a mechanism of food shortage for which Lack's hypothesis would be tenable. Ryder (1970) noted that when female Ross' Geese (*Chen rossii*) arrived on their arctic breeding grounds, there was little food available, and females relied almost exclusively on nutrient reserves that they had carried with them from farther south. These nutrient reserves represented a fixed amount of "food resources" that were used for both egg formation and maintenance costs during laying and incubation. Clearly, in this scenario, any additional investment in egg size (assuming greater nutrient content) could only come at the expense of fewer eggs and/or fewer reserves available for incubation. Ryder's hypothesis provided a rationale for extending Lack's analysis to intaspecific trade-offs in clutch size and egg size; i.e., females that lay large eggs on fixed nutrient budgets should, on average, produce smaller clutches (Rohwer and Eisenhauer 1989).

This notion of a trade-off between clutch size and egg size has figured prominently in theoretical life-history models (e.g., Smith and Fretwell 1974, Brockelman 1975, Winkler and Wallin 1987); however, empirical studies have not generally supported Lack's hypothesized trade-off (e.g., Rohwer 1988, Rohwer and Eisenhauer 1989, Lessells *et al.* 1989). One weakness of these studies is that the investigators did not manipulate any of the variables of interest; i.e., food (or nutrient reserve) availability, clutch size, or egg size. In this situation, phenotypic correlations can be misleading because individual variation in resource availability may overshadow any evidence of trade-offs (e.g., Smith 1981, Reznick 1985, Nur 1988*b*).

In this chapter, I assess numerous sources of variation in laying date, clutch size, and egg size of American Coots in attempt to test some of the preceding hypotheses.

3.2 METHODS

3.2.1 *Nesting studies.*

Initiation dates for most nests were determined by back-dating from incomplete clutches found during egg-laying, assuming a laying rate of 1 egg per day (e.g., Sooter 1941, Gullion 1953; see also Section 3.3.6). Occasionally, initiation dates were estimated by back-dating from known hatching dates, or by floating or candling eggs to determine stage of embryo development (Westerkov 1950, Weller 1956).

Clutch size was determined after laying had ceased for two consecutive days, provided that eggs were being incubated. Eggs known to have been parasitically-laid (see Appendix 2) were subtracted from clutch size, and known cases of egg loss were added to clutch size (these represented partial clutch destruction by predators, conspecific egg destruction by neighboring coots, eggs that fell into the water, or eggs inadvertently damaged by an observer). I could not unambiguously identify renesting attempts because laying birds were not individually marked; however, I have identified "potential renests" as those nests initiated in close proximity to a nest that had previously been destroyed. In 1990, I also used eggshell characteristics (color and spotting pattern) to identify renests. Individual coots produced highly consistent eggs (Appendix 2); these data helped verify that virtually every nest initiated < 30 m from a previously destroyed nest represented a renesting attempt. I recognized two types of renesting attempts: regular renests were nests initiated > 2 days after the last egg had been laid in the previous nesting attempt, whereas continuation nests were initated ≤ 2 days after destruction of a laying stage nest (i.e., I allowed a 1 d laying skip because birds had to construct a new nest). In 1990, I experimentally induced females to renest by removing their clutches at various times during the laying or incubation cycle.

I assessed egg size from linear measurements of length and maximum breadth (L and B, ± 0.05 mm). I calculated egg volume (cm^3) using Hoyt's (1979) equation: $\text{Volume} = 0.000507*L*B^2$. Length, maximum breadth, and estimated egg volume were relatively free of measurement error (Appendix 3) and egg volume was an excellent predictor of fresh egg mass ($r^2 = 0.96$, $P < 0.0001$, $n = 322$).

I calculated daily egg-laying rates based on the number of detected laying skips divided by the number of observation days (skips could only be detected in the interval between two nest visits, where both visits occurred during the egg-laying period); the standard error of this proportion was calculated using the formula provided by Johnson (1979).

I conducted egg-removal experiments to determine if clutch size was limited by the ability of coots to lay additional eggs (e.g., Klomp 1970). Egg-removal experiments involved removal of the fourth through ninth eggs (six total eggs) on the days they were laid; the first through third eggs, and all eggs after the ninth, were allowed to accumulate in the nest. Hence, for the first nine eggs they laid, laying females returned to find three or fewer eggs in their clutch. Removal experiments are intended to trick the female into thinking she has laid fewer eggs, but this requires that females assess their clutch size by visual or tactile cues (Steen and Parker 1981). If females "count" their eggs based on the physiological process of laying them, then removal experiments are unlikely to work (this form of "counting" could involve conscious recognition or, more likely, a passive physiological mechanism such as development of a fixed number of ovarian follicles; Klomp 1970, Parsons 1976, Moss and Watson 1982). Egg removal experiments are more likely to trick birds' sensory or physiological counting systems if removals begin with the earliest laid eggs (Klomp 1970, Parsons 1976, Duncan 1986), but birds are also more likely to abandon as a result of early manipulations (Rohwer 1984, 1986*c*).

3.2.2 *Statistical analyses.*

Variations in laying date, clutch size, and egg size were compared among years and among supplemental-feeding regimes using ANOVAs and ANCOVAs (PROC GLM, SAS Institute Inc. 1985). Similar analyses were employed for egg-removal experiments. Egg-laying rates (skip-rates) were compared among study groups using procedures described by Johnson (1979). Among-wetland variation in laying date, clutch size, and egg size was analyzed using nested-ANOVA (PROC NESTED). Due to uneven replication among wetlands, significance levels for these analyses had to be calculated using the GLM procedure. Years were analyzed separately due to annual variation in study area boundaries. During years with supplemental feeding experiments, wetland effects were nested within feeding effects. These analyses included any wetlands with two or more independent data points (i.e., renests were excluded).

Variation in egg size was partitioned into among- and within-clutch components using Model II (nested) ANOVA on all clutches with ≥ 4 measured eggs. This technique estimates the intraclass correlation coefficient (r_i, repeatability) of egg-size variation among clutches (e.g., Lessells and Boag 1987). Because I excluded known parasitic eggs and suspected renests from these data, "clutch" effects are largely synonymous with "female" effects. For a subsample of data from known renests (mostly from 1990), I was able to assess clutch and female effects independently. I also assessed individual repeatability of clutch size between first nests and renests.

3.3 RESULTS

I determined laying date and clutch size for 987 and 745 nests, respectively. Measurements were obtained for 5032 eggs from 786 clutches (4276 eggs from 674 first clutches and 756 eggs from 112 renests).

For first nests, most variation in egg size occurred among, rather than within, clutches; intraclutch repeatability was 63.3% for egg length, 61.0% for egg breadth, and 64.7% for egg volume (Table 3.1). Within-clutch repeatability (r_i) of egg volume ranged from 45.2 to 75.0% among sample groups (Table 3.1). Repeatability showed no obvious variation among years, but was substantially higher among corn-fed treatments in all 3 years (sign test, 4 treatment pairs, $P = 0.06$, 1 tailed). This effect was apparent for both length and breadth. Arnold (1991) demonstrated, with a somewhat different approach, that within-clutch

Table 3.1. Among- and within-clutch variation in length, breadth, and estimated volume of American Coot eggs[a].

	Length		Breadth		Volume		df
Group[b]:	Among	Within	Among	Within	Among	Within	Among,Within
M81CTRL	62.35	37.65	71.43	28.57	75.02	24.98	22,163
M85CTRL	60.43	39.57	53.08	46.92	60.86	39.14	19,179
M86CTRL	67.63	32.37	60.12	39.88	64.18	35.82	41,317
M87CTRL	67.73	32.27	69.65	30.35	71.38	28.62	76,551
M87CORN	73.29	26.71	75.02	24.98	79.82	20.18	26,227
M87TROUT	37.41	62.59	66.93	33.07	63.79	36.21	30,236
M87C+T	66.81	33.19	69.20	30.80	74.41	25.59	20,159
M88CTRL	66.11	33.89	47.04	52.96	51.07	48.93	99,556
M88FED	60.53	39.47	69.66	30.34	67.05	32.95	66,344
M89CTRL	34.15	65.85	50.85	49.15	45.17	54.83	18,136
M89FED	63.76	36.24	70.88	29.12	73.42	26.58	16,113
M90CTRL	60.78	39.22	62.72	37.28	65.62	34.38	88,711
Combined	63.33	36.67	60.98	39.02	64.69	35.31	564,3692

[a] Based on nested ANOVA (PROC NESTED, SAS Institute Inc. 1985).

[b] Sample group mnemonics: M stands for Minnedosa, numerals designate year (e.g., 87 is 1987), and terminal letters designate supplemental feeding treatments (CTRL = control [unsupplemented], CORN = corn, TROUT = trout chow, C+T = corn and trout chow, MIX = mixed diet of 1988 and 1989; see Section 2.3 for full details).

variation (SD) was lower among supplementally-fed coots, and he attributed this to a tendency for unsupplemented coots to occasionally produce relatively small eggs. Because eggs within clutches were not statistically independent, I used the mean from all measured eggs in a clutch for future analyses of among-female variation in egg size (nested ANOVAs, controlling for clutch and female effects, could not be used because they exceeded the memory capacity of SAS).

Laying date, clutch size, and mean egg volume exhibited large amounts of phenotypic variation (Fig. 3.1). Laying date ranged from 30 April to 25 June (57 d range), but two-thirds of all clutches were initiated over a 2-week period (10 - 23 May). Likewise, clutch size ranged from 3 to 19, but two-thirds of all clutches contained 8 - 11 eggs. Egg size was less variable than clutch size (CV's = 8.2 and 23.6 %, respectively), but egg size nevertheless accounted for 19% of the variation in clutch mass and was therefore an important component of total reproductive investment.

3.3.1 *Annual variation in laying date, clutch size, and egg size of control birds.*

Variances in clutch size and egg size were homogeneous among years (F_{max} = 1.60, $P > 0.05$; F_{max} = 1.85, $P > 0.05$; respectively), but annual variation in laying date was significantly heterogeneous (F_{max} = 10.32, $P < 0.01$). This effect remained significant if 1985, a year with very little data, was eliminated (F_{max} = 4.88, $P < 0.01$). There was significant annual variation in mean laying date, mean clutch size, and mean egg size (Table 3.2). Laying commenced relatively early in 1985 (this may have been an artifact of low sample size) and relatively late in 1988 and 1990; there was an 11 d range in mean laying date from the earliest to the latest year (Table 3.2). Clutch sizes were relatively large in 1985 and 1986, and relatively small during 1987-89. The maximum annual difference was 2.5 eggs (a 29.1% net increase from smallest to largest). Eggs were relatively large in 1986 and 1990, and they were relatively small in 1989 (Table 3.2), but the maximum annual difference of 1.55 g represented a net change of only 5.5%. Although laying date, clutch size, and egg size were often intercorrelated within years (see beyond), annual means of these variables were not statistically related

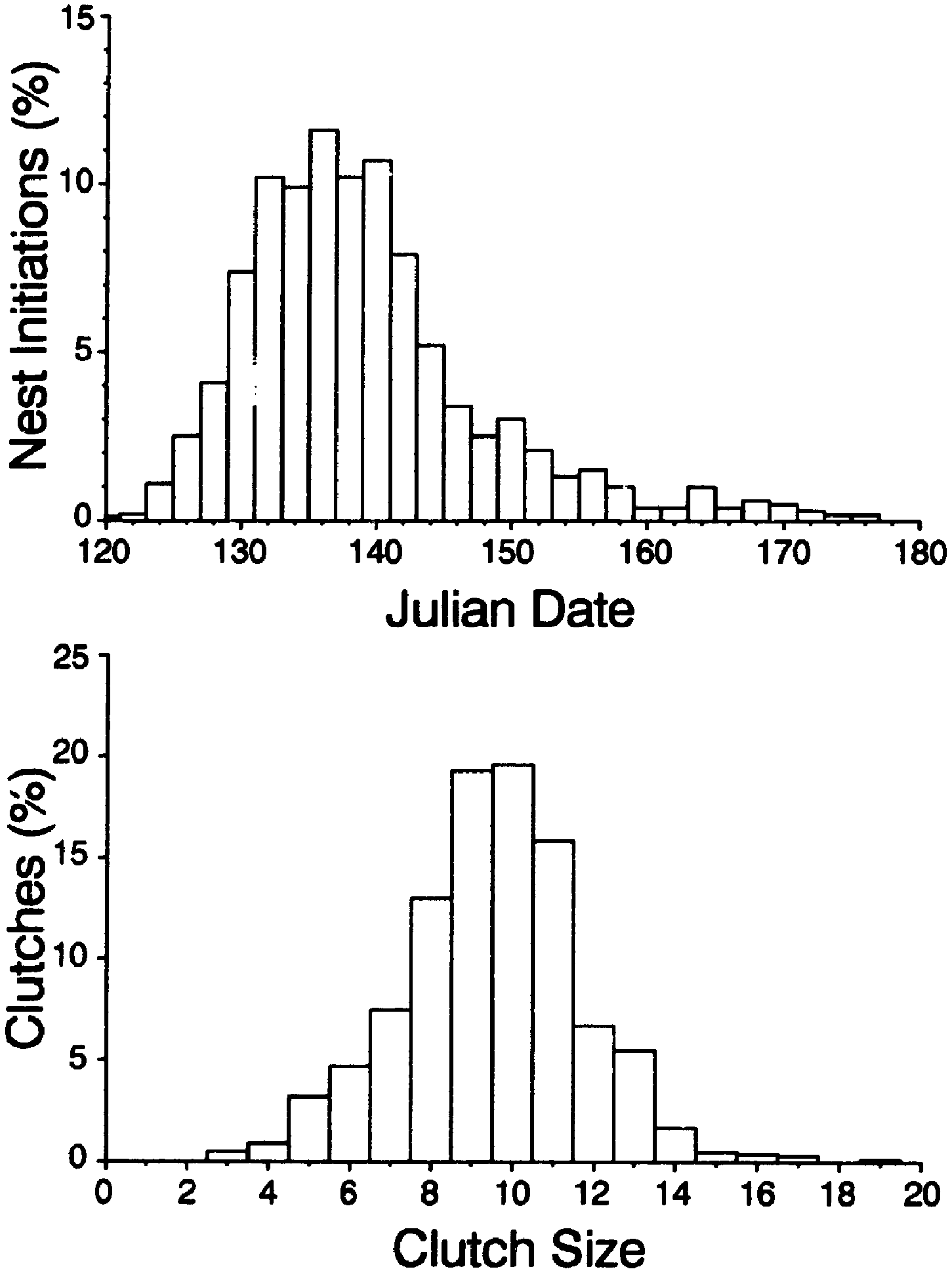

Fig. 3.1. Observed phenotypic variation in laying date (top) and clutch size (bottom). Data are from all unsupplemented clutches from all years, including renests. Data for laying date are pooled by 2 d intervals. Day 120 = 30 April, Day 180 = 29 June.

Table 3.2. Annual (among year) variation in laying date, clutch size, and egg size (mean + 1 SD [n]) of first nesting attempts of American Coots nesting at Minnedosa (control groups only).

Year	Laying Date[a]	Clutch Size	Egg Size[b]
1985	130.2 ± 3.3 d (15)	11.0 ± 1.6 (13)	27.8 ± 2.6 (22)
1986	135.6 ± 4.9 d (62)	11.1 ± 1.6 (94)	28.3 ± 1.9 (63)
1987	137.6 ± 10.6 d (30)	8.8 ± 1.8 (29)	27.3 ± 2.1 (37)
1988	139.7 ± 6.9 d (239)	8.6 ± 1.9 (154)	27.8 ± 2.3 (141)
1989	136.3 ± 4.8 d (29)	8.6 ± 1.8 (21)	27.1 ± 2.6 (27)
1990	141.6 ± 6.0 d (101)	9.8 ± 1.5 (72)	28.7 ± 2.1 (100)
Pooled[c]	136.6 ± 3.9 d (6)	9.7 ± 1.2 (6)	28.0 ± 0.7 (6)
Pooled[d]	138.9 ± 7.0 d (476)	9.5 ± 2.0 (383)	28.1 ± 2.3 (418)
Year effect[e]	13.53, < 0.0001	128.41, < 0.0001	3.91, 0.0008

[a] Julian dates

[b] Estimated volume (cm^3)

[c] Mean ± 1 SD of annual means (number of years).

[d] Mean ± 1 SD of all clutches.

[e] ANOVA results: F, P.

(DATE *vs.* CS: $r = -0.57$, $P = 0.24$; DATE *vs.* ES: $r = -0.61$, $P = 0.20$; CS *vs.* ES: $r = 0.02$, $P = 0.97$), probably due to the relatively small number of years involved ($n = 6$).

3.3.2 *Seasonal variation in clutch and egg size.*

I used ANCOVAs to examine among-year variation in clutch and egg size while controlling for variation in laying date. Clutch size declined seasonally during all years except 1985 and 1986 (Fig. 3.2, Table 3.3). The lack of an effect in 1985 could be attributed to small sample size, because the effect size was larger than in other years; however, samples were adequate in 1986, so the lack of a date effect must be interpreted as real. Variation in laying date accounted for 19% of the overall variation in clutch size, but ANCOVA revealed significant unexplained variation in clutch size among years (i.e., differences in slopes and intercepts; Fig. 3.2, Table 3.3). Least square means (controlling for variation in laying date) were similar to means for the raw data in all years except 1985 (Tables 3.2 and 3.3).

Mean egg volume did not vary with laying date when data were pooled for analysis ($F_{(1,700)} = 0.29$, $P < 0.59$), but egg volume declined with date when sample groups were included in the regression model (i.e., ANCOVA; date effect, $F_{(1,690)} = 10.84$, $P = 0.001$; group effect, $F_{(10,690)} = 4.95$, $P = 0.0001$). Egg size declined with date in 11 out of 12 sample groups (sign test, $P < 0.003$), but this relationship was significant only within the 1988-fed and the 1989-control groups (Table 3.4). Rates of seasonal decline in egg size did not differ among sample groups (group * date effect, $F_{(10,680)} = 1.00$, $P = 0.44$).

3.3.3 *Trade-off between egg size and clutch size.*

Mean egg volume varied significantly with clutch size, and this relationship differed significantly among sample groups (Table 3.4: ANCOVA; group * CS effect, $P = 0.0004$). Overall, egg volume increased by 0.15 cm^3 for each additional egg in the clutch ($r^2 = 0.023$, $P = 0.0003$); however, only four groups exhibited significant relationships between clutch size and egg size. In the

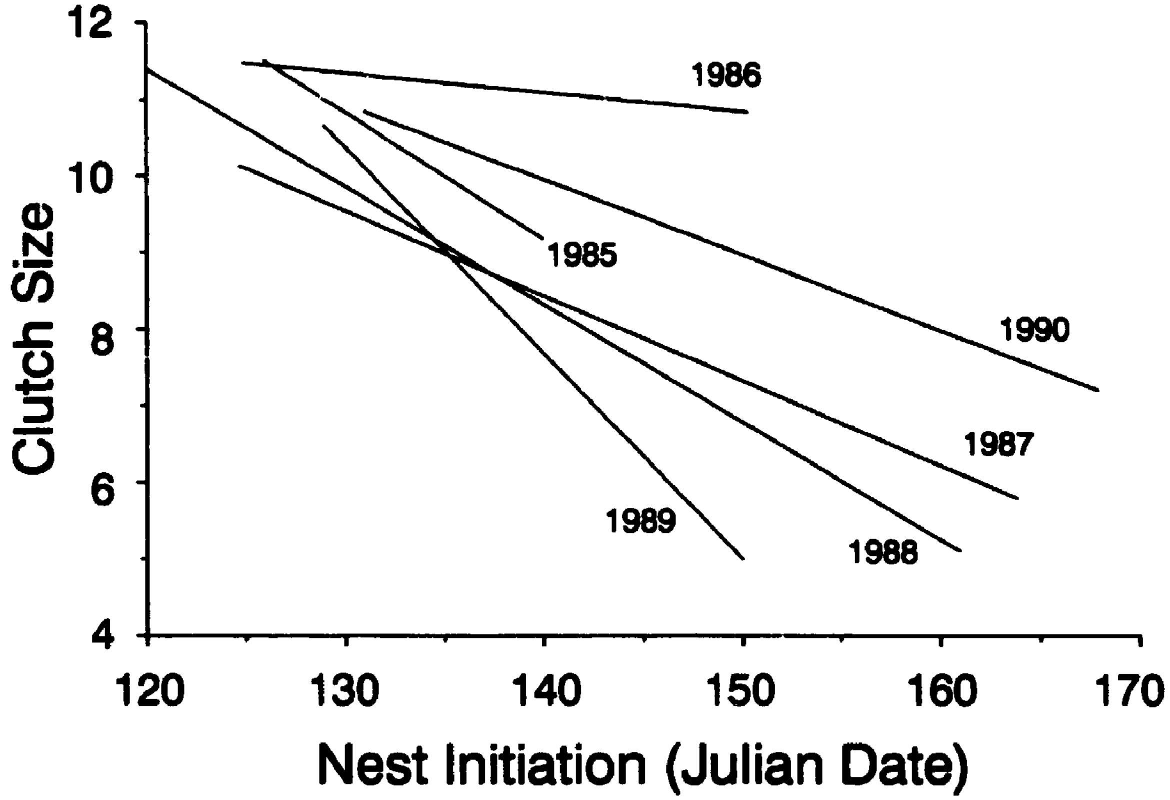

Fig. 3.2. Annual covariation in clutch size and laying date of American Coots. Data are from initial clutches of unsupplemented birds. Regression equations are described in Table 3.3. Day 120 = 30 April, Day 170 = 19 June.

Table 3.3. Annual covariation in laying date and clutch size for first nesting attempts of American Coots at Minnedosa (unsupplemented groups only).

	LS Clutch	Regression of clutch size on laying date:			
Year	Size[a]	a	b ± SE	r^2	P
1985	9.5 ± 7.1 (13)	34.11	-0.18 ± 0.25	0.045	0.49
1986	11.1 ± 1.6 (58)	13.58	-0.02 ± 0.04	0.004	0.64
1987	8.6 ± 1.5 (28)	23.69	-0.11 ± 0.03	0.346	0.001
1988	8.6 ± 1.5 (154)	29.73	-0.15 ± 0.02	0.329	0.0001
1989	8.3 ± 1.6 (21)	45.48	-0.27 ± 0.09	0.329	0.007
1990	10.0 ± 1.9 (72)	23.55	-0.10 ± 0.04	0.096	0.008
Pooled[b]	.-- (6)	12.02	-0.14 ± 0.13	0.228	0.34
Pooled[c]	.-- (346)	27.33	-0.13 ± 0.01	0.194	0.0001
Year effect[d]	2.11, 0.06				
Date effect	10.85, 0.001				
Interaction	2.60, 0.03				

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[a] Least square mean clutch size, controlling for among-year variation in laying date. Standard deviations based on raw data. Sample size in parentheses.

[b] Regression of mean annual clutch size on mean annual laying date (n = 6 years).

[c] Regression of clutch size on laying date for all nests from all years combined (note that the year by date interaction was significant).

[d] ANCOVA results: F, P.

Table 3.4. Relationships between egg size and laying date, and egg size and clutch size, among different samples of American Coots. Significant correlations are in boldface.

	Egg size vs. date			Egg size vs. clutch size		
Group:	n	r	P	n	r	P
M85CTRL	22	-0.27	0.23	17	-0.17	0.51
M86CTRL	60	-0.11	0.42	**58**	**0.33**	**0.01**
M87CTRL	36	0.31	0.36	**40**	**0.46**	**0.003**
M87TROUT	27	-0.21	0.29	29	0.35	0.06
M87CORN	26	-0.29	0.14	25	0.29	0.16
M87C+T	23	-0.24	0.28	**24**	**-0.57**	**0.004**
M88CTRL	141	-0.13	0.13	123	0.07	0.42
M88FED	**113**	**-0.18**	**0.05**	**97**	**0.23**	**0.02**
M89CTRL	**27**	**-0.45**	**0.02**	24	0.22	0.29
M89FED	17	-0.38	0.13	14	0.39	0.17
M90CTRL	100	-0.12	0.21	113	-0.08	0.38
Combined:	702	-0.02	0.59[a]	**564**	**0.15**	**0.0003**

[a] Significant when group effects are controlled; see the text.

M86CTRL, M87CTRL, and M88FED groups, egg size increased with clutch size (a similar trend was apparent within the M87TROUT group, P = 0.06), whereas these two variables were negatively correlated in the M87C+T group (Table 3.4).

There were no multi-way interactions among egg size, clutch size, and laying date, either in the combined data (P ≥ 0.16), or within and among sample groups (P ≥ 0.47). Nor was the relationship between clutch size and egg size an artifact of variation in laying date (which, in the previous section, was shown to be correlated with both variables). In combined variable analyses, clutch size was affected by laying date (mostly negative correlations, though this relationship varied among sample groups) and, in some sample groups, by egg size (mostly positive correlations). Egg size, however, was unaffected by laying date (P = 0.11), thus the previously described seasonal decline in egg size seems more related to changes in clutch size than to changes in laying date *per se*.

3.3.4 *Effects of supplemental feeding on laying date, clutch size, and egg size.*

In 1987, nest initiation was advanced among birds receiving supplemental corn or supplemental trout chow (P = 0.04 and 0.02, respectively). Effect sizes for corn and trout chow supplements averaged 2.8 and 3.1 days, respectively (Table 3.5), in a nesting season that spanned 42 days. These effects were independent (P = 0.55, Table 3.5); i.e., coots receiving both corn and trout chow nested about 6 days earlier than did controls. Supplemental feeding effects on laying date were not significant in 1988 or 1989, despite substantially larger sample sizes in 1988, and similar sample sizes in 1989 (Table 3.5). Effect sizes in 1988 and 1989 were 0.9 and 0.5 days, repectively, relative to nesting seasons of 46 and 26 days. In a combined analysis of 1987-1989 data (pooling M87TROUT, M87CORN, and M87C+T to create a single 1987 fed group), year and feeding effects were both significant (P < 0.0001, maximum effect size = 6.0 d [1987 *vs.* 1988]; P = 0.01, effect size = 1.4 d; respectively), and there was a near-significant interaction effect (P = 0.07, feeding effects in 1987 tended to be stronger than in 1988 and 1989) (Table 3.5).

In 1987, clutch size increased among coots receiving supplemental corn, but

Table 3.5. Effects of supplemental corn and supplemental trout chow on laying dates and clutch sizes of American Coots.

Group:	Laying Date[a]	Clutch Size	Egg Size[b]
1987			
M87CTRL	136.1 ± 1.5 d (43)[c]	8.8 ± 0.3 (29)	27.3 ± 0.3 (37)
M87TROUT	132.3 ± 1.0 d (29)	9.4 ± 0.5 (17)	27.5 ± 0.4 (27)
M87CORN	132.6 ± 1.4 d (28)	10.1 ± 0.5 (16)	27.5 ± 0.6 (26)
M87C+T	130.4 ± 0.6 d (25)	10.3 ± 0.4 (13)	27.9 ± 0.6 (23)
Corn effect:	4.54, 0.04, -2.8[d]	7.31, 0.009, +1.2	0.65, 0.42, +0.34 cm^3
Trout effect:	5.50, 0.02, -3.1	1.36, 0.25, +0.5	0.38, 0.54, +0.26 cm^3
Corn * Trout:	0.35, 0.55, --	0.13, 0.72, --	0.03, 0.86, --
1988			
M88CTRL	139.7 ± 0.5 (254)	8.6 ± 0.2 (154)	27.8 ± 0.2 (141)
M89MIX	138.8 ± 0.5 (222)	9.4 ± 0.2 (142)	27.9 ± 0.2 (113)
Food effect:	1.63, 0.20, -0.9	12.16, 0.0006, +0.8	0.01, 0.93, +0.03 cm^3
1989			
M89CTRL	136.3 ± 1.0 (29)	8.6 ± 0.6 (21)	27.1 ± 0.5 (27)
M89MIX	135.8 ± 1.2 (20)	9.0 ± 0.7 (14)	26.8 ± 0.4 (17)
Food effect:	0.14, 0.71, -0.5	0.18, 0.67, +0.4	0.21, 0.65, -0.33 cm^3
1987-89			
CTRL[e]	138.9 ± 0.4 (326)	8.7 ± 0.2 (221)	27.6 ± 0.2 (232)
FED[e]	136.9 ± 0.4 (324)	9.5 ± 0.2 (185)	27.7 ± 0.2 (179)
Food effect:	6.37, 0.01, -1.4	17.25, 0.0001, +0.8	0.12, 0.73, +0.10 cm^3
Year effect:	33.02, 0.0001, --	2.63, 0.07, --	3.08, 0.05, --
Year * food:	2.65, 0.07, --	0.50, 0.60, --	0.38, 0.68, --

[a] Values are Julian dates; 121 = 1 May.

[b] Estimated volume (cm^3).

[c] Values are means [least square means for combined data] ± 1 SE (n).

[d] F, P, effect size (in d, eggs, and cm^3, for date, clutch size, and egg size, respectively).

[e] M87TROUT included with fed groups for laying date, and with control groups for clutch size and egg size.

not among birds receiving trout chow (Table 3.5). A clutch size increase was also detected among coots receiving mixed supplemental food in 1988, but not in 1989 (Table 3.5). Effect sizes averaged 1.2 and 0.5 eggs in 1987 (corn and trout chow, respectively), 0.8 eggs in 1988, and 0.4 eggs in 1989. Because increases in clutch size among supplementally-fed coots were always accompanied by earlier laying dates (even though these effects were not always significant), changes in clutch size may have been correlated responses to changes in laying date (e.g., Daan et al. 1988). To test this possibility, I conducted ANCOVAs using laying date as a covariate.

There was a significant interaction effect among corn, trout chow, and laying date in the 1987 feeding experiment; clutch sizes of coots receiving both food types did not exhibit a seasonal decline, whereas clutch sizes of the other three groups did (Fig. 3.3*a*). This interaction effect could be attributed to two clutches, each containing 11 eggs, laid on days 147 and 152 by coots receiving combined corn and trout chow supplements (Fig. 3.3*a*). Because this effect was based largely on two data points and was not strongly significant ($P = 0.03$), and because no other analyses suggested a synergistic effect of corn and trout chow, I deleted this three-way interaction effect and fit a reduced model to the data. With the three-way interaction deleted, the ANCOVA model was reduced to significant date ($P < 0.0001$) and corn ($P = 0.0005$) effects (Fig 3.3*b*).

The 1988 feeding experiment generated almost identical results (Fig. 3.4*a*). Clutch size was affected by date and food ($P < 0.0001$ for each), but there was no interaction effect ($P = 0.27$). Figure 3.4*a* can be almost perfectly superimposed on Figure 3.3*b*; if 1987 and 1988 data are combined (treating M87CTRL and M87TROUT as controls and M87CORN and M87C+T as fed), year effects are almost nonexistant ($P > 0.72$, regression lines are displaced by less than one day for fed and control coots).

The 1989 feeding experiment generated qualitatively different results. Clutch size declined much more rapidly with laying date, and there was no effect of supplemental food on clutch size (Fig. 3.4*b*).

When data from all three feeding experiments were analyzed jointly

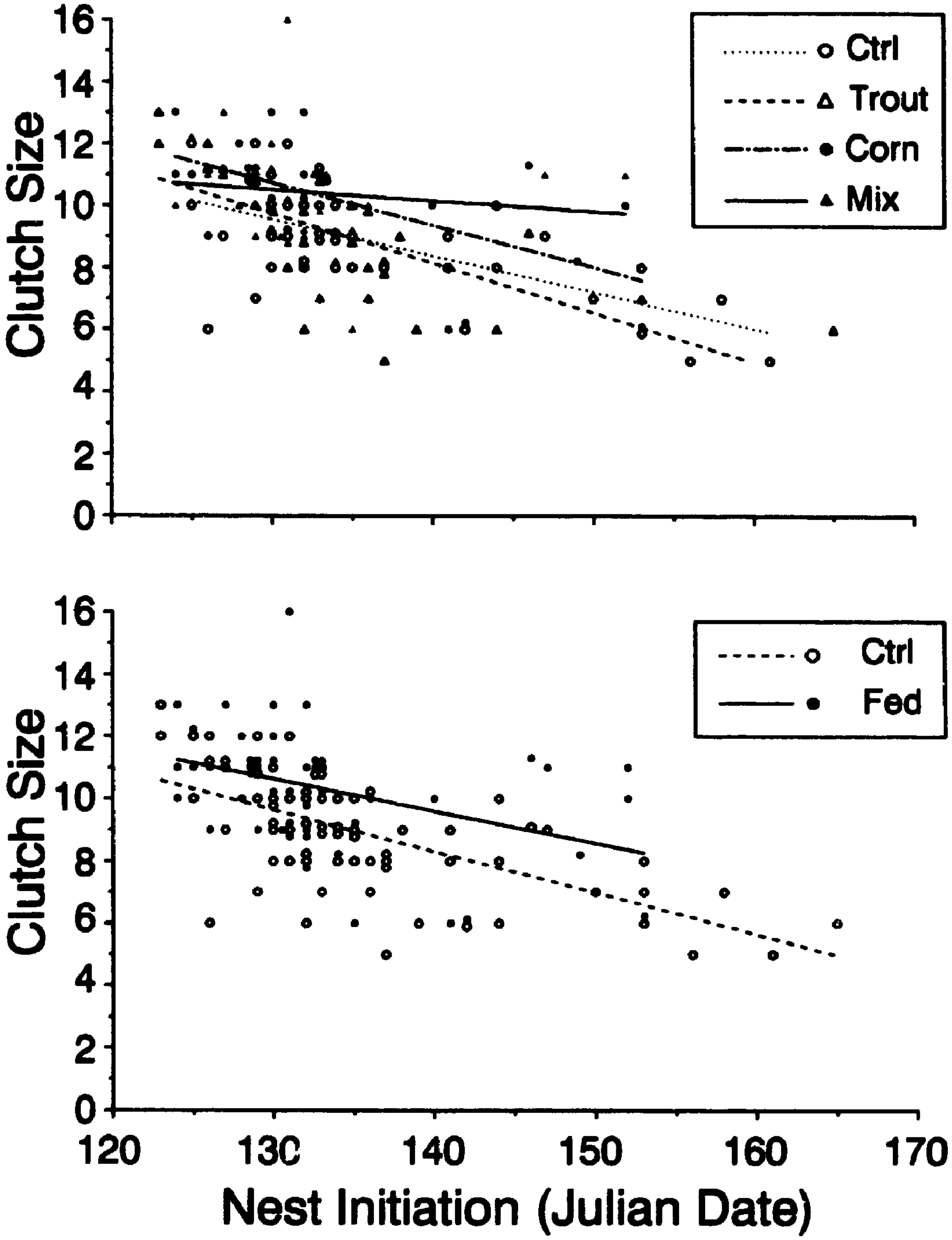


Fig. 3.3. Top: Effects of supplemental corn and trout chow on relationship between clutch size and laying date in 1987 (see text for discussion of significant corn * trout chow * date interaction). Bottom: Effect of supplemental corn on the relationship between clutch size and laying date in 1987 (Ctrl includes "true controls" plus trout chow; Corn includes corn plus mixed diet). Date and corn effects were both significant. Day 120 = 30 April, Day 170 = 19 June.

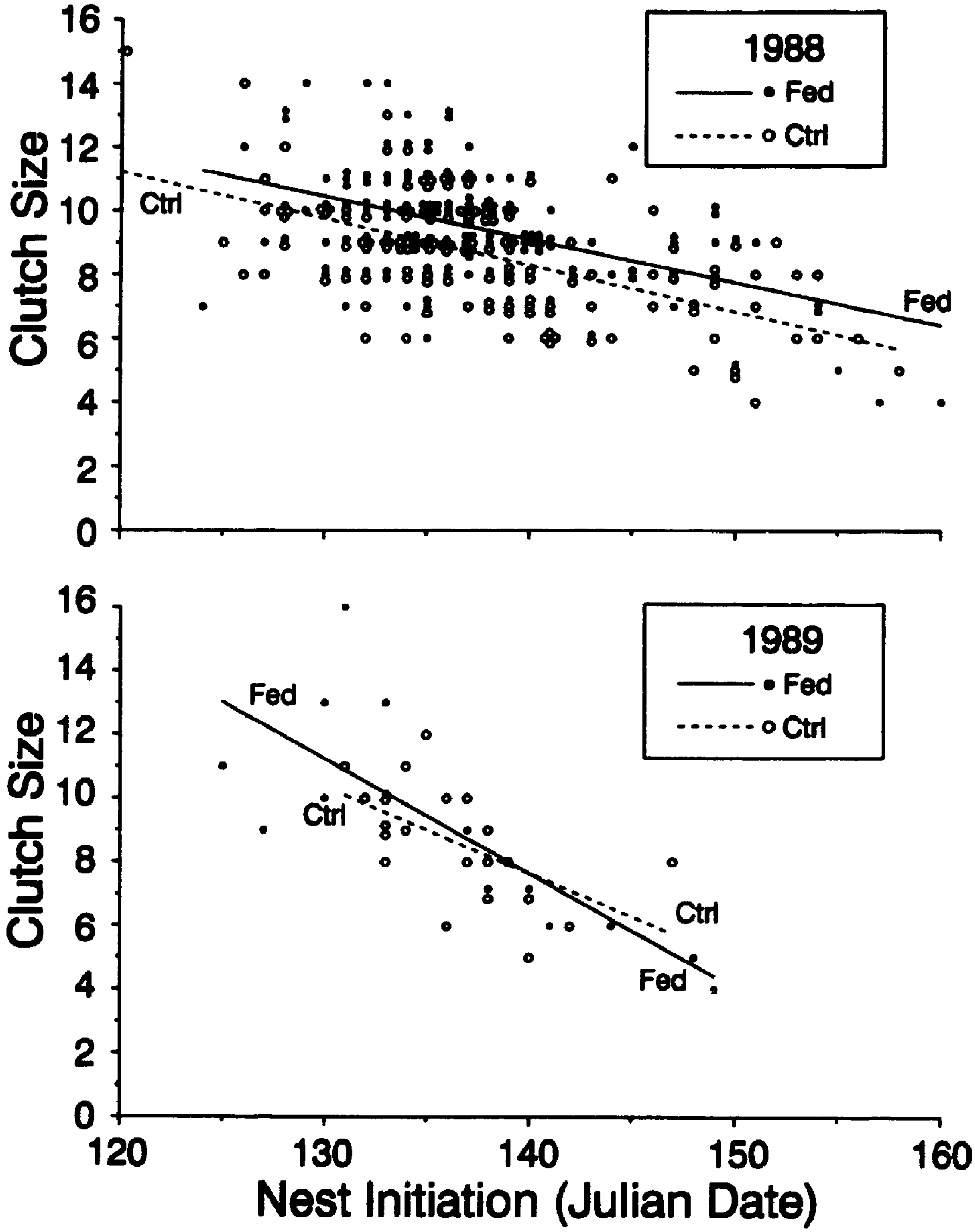


Fig. 3.4. Effects of supplemental food on relationships between clutch size and laying date in 1988 (top) and 1989 (bottom). Renests were excluded. Date effects were significant in both years, feeding effects in 1988 only, and date * food interactions in neither year (see text for details). In 1988, the quadratic term for laying date was nearly significant (F = 3.48, P = 0.06). Day 120 = 30 April, Day 160 = 9 June.

(treating M87CORN and M87C+T as fed treatments and M87CTRL and M87TROUT as controls), effects of date, year, year * date, and food were all significant, but food * year, food * date, and food * year * date effects were not (Table 3.6). This suggests that the absence of a supplemental feeding effect in the 1989 experiment may have been due to small sample size and lack of statistical power, rather than a truly different relationship between food supply and clutch size in that year.

Supplemental feeding had no detectable influence on egg size (Table 3.5; P ≥ 0.42).

3.3.5 *Among-wetland variation in laying date, clutch size, and egg size.*

Date of nest initiation varied among wetlands supporting ≥ 2 nesting pairs in 1985, 1988, and 1990, and nearly so in 1986 (Table 3.7). Clutch size was less variable among wetlands, differing only in 1987. Among-wetland variation in clutch size for 1987 became more pronounced if clutch size was corrected for variation in laying date, and in addition, wetland effects on clutch size became significant in 1988 when variation in laying date was removed (Table 3.7). Egg size did not differ among wetlands, although results were close to significance in 1989 (Table 3.7; P = 0.09). For the 1987, 1988, and 1989 data, wetland effects were nested within feeding treatment effects. Effects of supplemental feeding on laying date and egg size were not significant in any year (P ≥ 0.13 and 0.24, respectively), but clutch size was influenced by food in two of three analyses (1987: P = 0.03, 1988: P = 0.0002, 1989: P = 0.50).

3.3.6 *Variation in laying rates.*

Skip-rates ranged from 0.0% in the M85CTRL group to 7.1% in the M89MIX group (Table 3.8). In 1988, skip-rates were significantly lower among supplementally fed coots (Table 3.8) and in 1987, skip-rates were lower among birds receiving supplemental corn (M87CORN and M87MIX *versus* M87CTRL and M87TROUT; skip-rate = 0.026 ± 0.11 (1 SE) *vs.* 0.058 ± 0.016, respectively). The opposite trend was apparent in the 1989 feeding experiment,

Table 3.6. Effects of laying date, year, and supplemental food on clutch size of first nesting attempts of American Coots, 1987-1989, Minnedosa, Manitoba.

Effect:	Parameter[a]	SS[b]	F	P
Date	-0.333	319.44	128.59	0.0001
Year	.--	32.93	6.63	0.002
Food	0.659	43.01	17.31	0.0001
Date*Year	.--	33.93	6.83	0.001
Date*Food	-0.005	1.40	0.04	0.84
Year*Food	.--	1.39	0.28	0.76
Date*Year*Food	.--	4.85	0.97	0.38
Model[c]	--	1644.29	43.98	0.0001

[a] Date and food effects only.

[b] Type III SS.

[c] Reduced model containing significant effects only.

Table 3.7. Among-wetland variation in laying date, clutch size, and egg size of American Coots[a].

	Laying date				Clutch size				Egg size			
Year:	% Var.	F	d.f.	P	% Var.	F	d.f.	P	% Var.	F	d.f.	P
1985	70.8	6.42	7,10	0.005	18.9	1.53	6,16	0.27	0.0	0.36	6,7	0.88
1986	21.7	1.75	15,28	0.10	0.0	0.85	19,46	0.64	0.0	0.99	7,12	0.48
1987[b]	0.0	0.84	26,66	0.68	29.7	2.37	23,59	0.004	0.0	0.82	24,68	0.94
1988[b]	13.8	1.76	84,335	0.0003[c]	3.6	1.16	62,207	0.22	5.6	1.22	52,146	0.18
1989[b]	0.0	0.95	20,27	0.51	0.0	0.89	8,23	0.52	23.7	1.93	10,26	0.09
1990	20.9	2.06	21,69	0.01	4.8	1.20	19,61	0.29	0.0	0.85	21,69	0.66

Note: based on nested-ANOVA of wetlands with $\geq$ 2 nest histories.

[a] Renests excluded unless data missing from first nest (used in egg size analyses only).

[b] Wetland effects nested within supplemental feeding effects.

[c] Had to delete data from 5 wetlands and 16 nests for PROC GLM to handle calculations.

Table 3.8. Incidence of laying skips among sample groups of American Coots.

Group:	Nests	Exposure[a]	Skips	Skip-rate[b]	SE[c]	95% CI[d]	LSD tests[e]
M85CTRL	16	114	0	0.000	0.006[f]	0.000 - 0.012[f]	A
M86CTRL	38	222	3	0.014	0.008	0.000 - 0.029	B
M87CTRL	23	106	7	0.066	0.024	0.018 - 0.114	FG
M87TROUT	19	100	5	0.050	0.022	0.006 - 0.093	DEFG
M87CORN	18	82	2	0.024	0.017	0.000 - 0.058	BCD
M87MIX	18	107	3	0.028	0.016	0.000 - 0.060	BCDE
M88CTRL	81	305	14	0.046	0.012	0.022 - 0.070	DEF
M88FED	75	315	8	0.025	0.009	0.008 - 0.043	BC
M89CTRL	19	32	1	0.031	0.031	0.000 - 0.093	CDEFG
M89FED	13	42	3	0.071	0.040	0.000 - 0.151	G
M90CTRL	63	259	8	0.031	0.011	0.009 - 0.053	CD

[a] Exposure is the number of observation days on which skips could have been detected, had they occurred.

[b] Skip-rate = skips/exposure.

[c] SE of skip rate = SQRT(((Exposure-Skips)*Skips)/Exposure^3); after Johnson 1979.

[d] 95% Confidence Interval: lower limits < 0 have been truncated.

[e] Groups followed by the same letter are not significantly different, based on mutual overlap of CI's with group means.

[f] SE and 95% CI calculated assuming 0.5 laying skips.

but this variation was not significant and was based on very few observation (Table 3.8). Combining data from 1987-89, fed birds had significantly fewer laying skips than did controls (fed birds: 0.029 ± 0.007; control birds [including M87TROUT]: 0.050 ± 0.009). In 1990, skip rates at first nests were significantly lower than skip rates at renests and continuation nests (1st nests: 0.017 ± 0.010; renests and continuation nests: 0.059 ± 0.026). Among groups, skip-rates were inversely correlated with mean clutch sizes (r = -0.75, P = 0.008, n = 11 sample groups); i.e., laying skips were most prevalent among sample groups producing small average clutches.

3.3.7 *Egg removal experiments.*

Coots that had six eggs experimentally removed from their nests during egg laying produced significantly more eggs than did unmanipulated controls (ANOVA on pooled data: P < 0.0001); however, they only replaced one of the six removed eggs, on average (Table 3.9). Removal effects were significant in the M85CTRL, M86CTRL, and M88CTRL groups (Table 3.9), and nearly so in the M88MIX group (P = 0.06). Egg-removal did not affect clutch size among any of the 1987 groups (Table 3.9), or among all 1987 groups combined (P = 0.34). Variance in clutch size of removal birds nearly always increased relative to controls (7/8 sample groups; sign test: P < 0.05); however, the F_{max} test was significant only for the pooled data. When all data were combined, there were no significant interaction effects between egg-removal and supplemental food or between egg-removal and year (Table 3.9). When I included laying date as a covariate in the preceding analyses, quantitatively similar results were obtained in almost all analyses. Exceptions included stronger removal effects in 1988 (including a statistically significant effect in the M88MIX group) and a significant year * removal effect in the overall data. Hence, the lack of a removal effect in 1987 reflected a statistically different population response in comparison to the other three years.

Mean egg volume and clutch size were weakly correlated among removal nests (r = 0.14, P = 0.24, n = 71 nests). This correlation remained insignificant

Table 3.9. Number of eggs laid by American Coots in response to experimental removal of six eggs during laying (X ± 1 SD [n]).

Sample group:	Control	6-egg removal	F	P	F_{max}[a]	P
M85CTRL	11.00 ± 1.60 (13)	12.86 ± 2.34 (7)	4.36	0.05	2.14	NS
M86CTRL	11.11 ± 1.61 (94)	12.27 ± 2.90 (11)	4.24	0.04	3.24	NS
M87CTRL	8.79 ± 1.78 (29)	8.89 ± 1.76 (9)	0.02	0.89	0.98	NS
M87TROUT	9.35 ± 2.12 (17)	9.43 ± 1.72 (7)	0.01	0.93	1.52	NS
M87CORN	10.06 ± 1.95 (16)	10.67 ± 2.58 (6)	0.35	0.56	1.75	NS
M87C+T	10.31 ± 1.38 (13)	10.75 ± 2.38 (8)	0.30	0.59	2.97	NS
1987***[b]	9.45 ± 1.91 (75)	9.87 ± 2.16 (30)	0.93	0.34	1.28	NS
M88CTRL	8.60 ± 1.93 (154)	10.08 ± 2.78 (12)	6.18	0.01	2.07	NS
M88MIX	9.38 ± 1.93 (142)	10.67 ± 2.55 (9)	3.60	0.06	1.75	NS
1988***[c]	8.97 ± 1.97 (296)	10.33 ± 2.63 (21)	8.94	0.003	1.78	NS
All data[d]	10.42 ± 2.07 (478)	11.41 ± 2.64 (69)	14.64	0.0001	1.63	< 0.05

[a] $F_{max} = s^2$ removal/s^2 control.

[b] 1987 sample groups combined due to lack of removal*supplemental feeding effect (F = 0.26, P = 0.61). Means are least squares estimates controlling for feeding effects; SD's are based on raw data.

[c] 1988 sample groups combined due to lack of removal*supplemental feeding effect (F = 0.05, P = 0.83). Means are least squares estimates controlling for feeding effects; SD's are based on raw data.

[d] 1985 - 1988 sample groups combined. Overall effects: Removal*Supplemental Food: F = 0.05, P = 0.83; Removal*Year: F = 1.45, P = 0.23; Removal*Supplemental Food*Year: F = 1.20, P = 0.31. Means are least squares estimates controlling for significant (P = 0.0001) year and feeding effects; SD's are based on raw data.

if it was based only on early-sequence (1 - 9) or late-sequence (10^+) eggs (early: $r = 0.14$, $P = 0.25$, $n = 70$ nests; late: $r = 0.10$, $P = 0.54$, $n = 38$ nests). When I based this correlation on standardized egg volumes, coots producing large clutches produced relatively large late-sequence eggs ($r = 0.35$, $P = 0.04$, $n = 37$).

3.3.8 *Renests and continuation nests.*

In 1990, 90 coot nests were destroyed, either experimentally or by natural causes. Destroyed nests were replaced by renest clutches in 73 cases (81%). Whether a female renested or not was independent of how many previous nests she had attempted (this varied from 1 to 5 among females), how many eggs she had laid in her previous nest, and the size of eggs in her previous nest (Table 3.10). The only variable significantly affecting renesting propensity was date of previous nest destruction ($P < 0.0001$; renesting propensity declined seasonally), although stage of nest destruction approached significance (Table 3.10, $P = 0.07$; nests late in incubation were less likely to be replaced, after controlling for the generally later date of destruction among these nests).

Renesting intervals (the length of time between destruction of the previous clutch and laying of the first egg in the replacement clutch) varied from 0 to 7 d. The most important factor influencing the length of a renesting interval was the stage at which the previous nest was destroyed. Nests destroyed during laying were often replaced the next day (interval = 0 d), whereas nests destroyed later in incubation required 4 to 7 d to replace (Fig. 3.5). This relationship was strongly curvilinear (Fig 3.5), as evidenced by the significant second-order regression term (Table 3.11). Renesting intervals were also affected by nest attempt (they declined as number of attempts increased) and by date of clutch destruction (they increased later in the year), but not by egg size in either the initial or the replacement clutch, initial clutch size, replacement clutch size (although this was almost significant [$P = 0.10$], birds with long renesting intervals tended to produce smaller clutches), or type of nest loss (investigator removals *vs.* natural losses) (Table 3.11).

Thirty birds produced two or more complete clutches (27 with two

Table 3.10. Factors affecting the renesting propensity of American Coots[a].

Effect:	df	χ^2	P	Order of Deletion
Intercept	1	16.32	0.0001	-26.07[b]
Date lost (D)	1	15.07	0.0001	+0.15[b]
Clutch size (CS)	1	0.06	0.80	13
Days incubated (I)	1	3.30	0.07	14
Nest attempt (N)	1	0.05	0.82	10
Egg size (ES)	1	0.01	0.91	8
D * CS	1	1.98	0.17	12
D * I	1	0.33	0.57	3
D * N	1	0.52	0.47	7
D * ES	1	.--	.--[c]	4
CS * I	1	1.35	0.24	11
CS * N	1	1.96	0.16	9
CS * ES	1	0.87	0.35	5
I * N	1	0.05	0.82	2
I * E	1	.--	.--[c]	1
N * E	1	0.19	0.67	6

[a] Maximum-likelihood ANOVA table from a logistic regression analysis (PROC CATMOD, SAS Institute Inc. 1985). Initial model included all main-effects and 2-way interactions. Nonsignificant effects were sequentially deleted based on examination of P values (least significant effects deleted first, unless contained within a higher-order interaction). χ^2 and P values are based on the iteration in which each effect was deleted (e.g., deletion order), or in the case of intercept and date lost, the final iteration.

[b] Model parameter for significant effects.

[c] Parameter unestimatable.

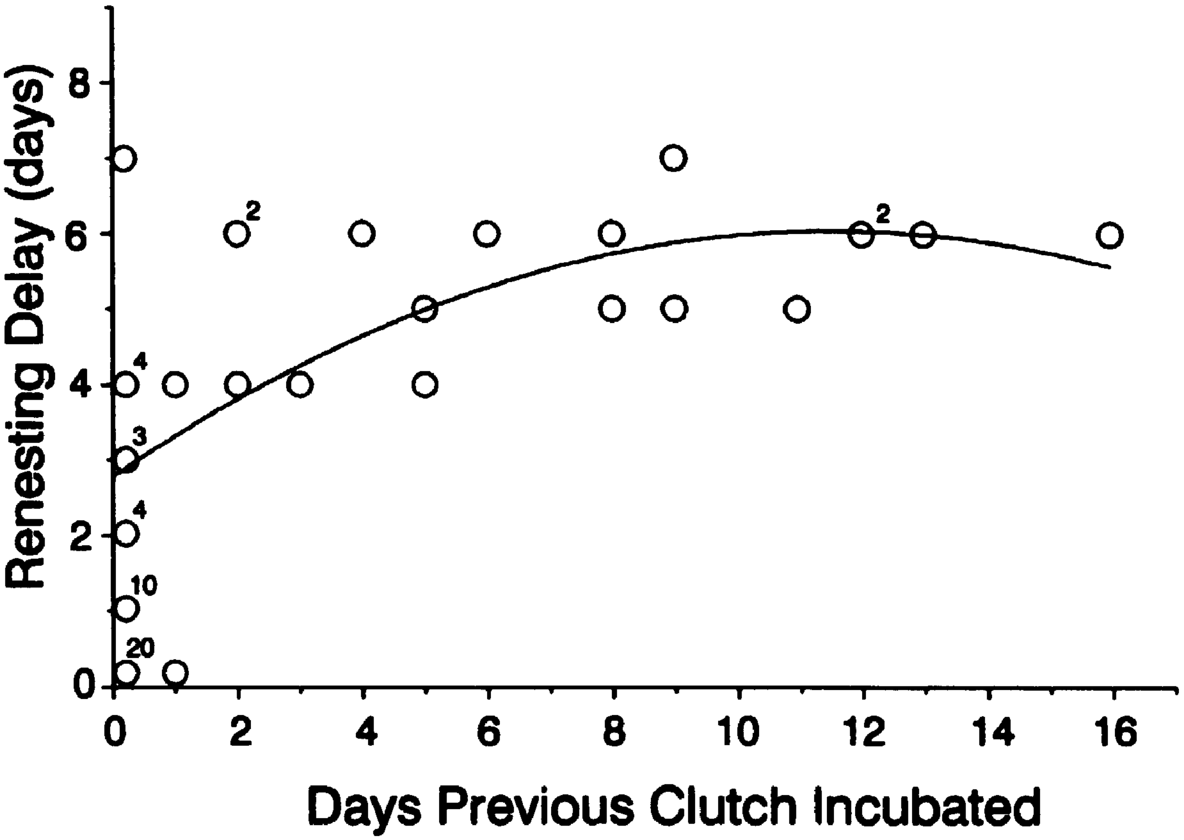


Fig. 3.5. Renesting delay of American Coots in relation to number of days the previous clutch had been incubated on the day of clutch destruction. All laying stage nests were assigned an abscissa of zero. Numerals beside data points indicate the number of multiple observations at that point. The fitted line represents a significant 2nd-order regression (see Table 3.11).

Table 3.11. Factors affecting the length of renesting delay (days) among American Coots[a].

Effect:	b	F	P	Order of Deletion
Intercept	-13.3	.--	0.01	.--
Days incubated	0.76	18.99	0.0001	.--
(Days incubated)^2	-0.041	9.05	0.004	.--
Date lost	0.11	8.01	0.007	.--
Nest attempt	-0.98	5.54	0.02	.--
Initial clutch size	.--	1.45	0.23	4
Initial egg size	.--	1.08	0.30	2
Renest clutch size	.--	2.73	0.10	5
Renest egg size	.--	0.00	0.98	1
Loss type[b]	.--	0.95	0.33	3

[a] Nonsignificant effects sequentially deleted from statistical model, and F and P values recalculated for remaining variables.

[b] Loss type: natural losses (e.g., predation, flooding, abandonment) *versus* experimental clutch removal.

clutches, 3 with three). Clutch size was somewhat repeatable among birds (repeatability = 21.8%, $F_{(29,33)} = 1.59$, $P = 0.10$), but renests tended to be smaller than initial nests (8.20 ± 2.70 *vs.* 9.27 ± 1.53, respectively; $F_{(1,61)} = 3.50$, $P = 0.07$). Because renests are necessarily produced later in the season than initial nests, smaller size of renest clutches could be an artifact of laying date. When both predictor variables were included in the regression model, only laying date explained significant variation in clutch size (P(*DATE*) = 0.001, P(*ATTEMPT*) = 0.19); in this analysis, renests were nonsignificantly larger than initial nests (by about 0.6 eggs). When I corrected for variation in clutch size due to laying date (by using residuals from a regression of CS on DATE), corrected clutch size was significantly repeatable among females (repeatability = 39.3%; $F_{(29,32)} = 2.36$, $P = 0.009$).

Some coots produced phenomenal numbers of consecutive or near-consecutive eggs; e.g., female 4029 laid 35 eggs in 37 days (4 different nests plus 2 parasitic eggs), female 4018 laid 34 eggs in 39 days (5 nests plus 3 parasitic eggs), and female 4009 laid 27 eggs in 28 days (3 nests) (see Appendix 4). Others produced very large replacement clutches following a long laying series in one or more earlier nests; e.g., female 4088 laid a 17 egg clutch after laying 3 eggs in a previous nest, female 4029 laid a 14 egg clutch after laying 21 eggs in three previous clutches (Appendix 4). In contrast, a few coots laid very small continuation clutches, and their combined total egg production was approximately one "normal" clutch of eggs; e.g., female 4094 laid 4 eggs in her first nest and only 5 eggs in a continuation nest. If I treated continuous sequences of eggs from ≥ 2 nests as "clutches" (separated by laying gaps of no more than 1 d), these continuation clutches were substantially larger than normal clutches (14.7 ± 5.9 [1 SD] eggs [range 5 - 27] *vs.* 9.8 ± 1.5 [Table 3.1]). These data for continuation clutches included two clutches of 5 and one of 7; with these deleted, the mean size of continuation clutches was 16.0 (these 3 clutches represented rapid back-to-back nest failures, and therefore cannot be considered complete clutches; moreover, such cases were excluded from "normal clutches" prior to analysis).

Egg size was highly repeatable between nesting attempts; female effects accounted for 47.4, 61.1 and 60.8% of the total variation in egg length, breadth, and volume, respectively, whereas clutch effects accounted for 9.9, 10.8, and 11.7% of this variation (significance levels could not be obtained for this analysis due to the complexity of the data set). Egg size was not smaller among renest and continuation clutches (mean egg size averaged 0.20 cm^3 smaller than in the previous clutch [representing a 0.7% decline]; Wilcoxon Matched-pairs Signed-rank Test, $P = 0.15$, $n = 69$ pairs). There was no trade-off between total number of eggs laid by renesting birds (Appendix 4) and the mean size of their eggs; in fact, the correlation was almost significantly positive ($r = 0.26$, $P = 0.07$, $n = 49$).

3.4 DISCUSSION

3.4.1 *Annual variation in laying date, clutch size, and egg size.*

Significant annual variation was detected for laying date, clutch size, and egg size, although this variation was rather slight for egg size. In addition, nesting seasons were longer in some years than others. Some of the annual variation in clutch size and egg size could be attributed to covariation with laying date and clutch size, respectively, but annual effects usually remained significant after partitioning out such sources of variation (see beyond).

Annual variation in laying date, clutch size, and egg size is often attributed to annual variation in food abundance (Gibb 1950, Bengtson 1971, Jarvinen and Väisänen 1984, Hussell and Quinney 1987, Korpimäki 1987, Perrins and McCleery 1989, Teather and Weatherhead 1989; but see Lyon et al. 1987). I did not assess annual variation in food abundance in this study (neither did some of the previous studies), but other lines of evidence (e.g., supplemental feeding) suggested that factors other than food availability were more likely to have influenced annual variation in laying date, clutch size, and egg size. However, annual variation in these traits was unrelated to spring water conditions, spring migrational chronology, and spring breeding densities (data from Table 2.2: $P \geq 0.09$, $k = 18$ correlations). Because of the small number of years involved in these analyses ($n \leq 6$), these correlations had very little power, especially if relationships among variables were complex.

In a 21 year study of a European Coot population in The Netherlands, Perdeck and Cavé (1989) demonstrated that early spring temperatures (February, March) explained approximately half of the annual variation in timing of breeding. They showed that temperature affected both arrival (due to ice-melt) and the "decision" to breed after coots had settled on territories. Annual variation in the termination of nesting activity was unrelated to when the nesting season had started, hence in warm springs when most pairs could begin nesting at an early date, the frequency of second broods increased because some birds had sufficient time to renest after raising their first broods (Perdeck and Cavé 1989). M. Sorenson (*pers. comm.*) found positive correlations between early spring (15 April - 15 May) temperatures and mean nesting dates of Canvasbacks (*Aythya valisineria*), Redheads (*A. americana*) and American Coots at Minnedosa (coot data were from this study), but the relationships were based on only three years of data.

3.4.2 *Seasonal variation in clutch and egg size.*

By far the most important factor affecting clutch size was covariation with laying date. This relationship showed pronounced annual variation; in 1986 laying date accounted for 0.4% of the variation in clutch size, whereas in 1987 it explained 34.6% of this variation. Annual rate of clutch size decline was independent of mean laying date (r = -0.31) and mean clutch size (r = -0.50), but seemed to vary with annual wetland conditions (Fig. 3.2: semipermanent pond depths in mid-May, r = -0.80; pond depths in mid-June, r = -0.88; pond depths in mid-July, r = -0.84; rate of water-loss from mid-May to mid-June, r = 0.52; and rate of water-loss from mid-May to mid-July, r = -0.11). Although the first three correlations were statistically significant, I consider six years of data insufficient to establish biological significance. These data suggest that coots may be adopting a "hurry up" approach to deteriorating water conditions (e.g., Clark and Wilson 1981), or that they may be investing less in reproduction when the likelihood of success is reduced by drought. These hypotheses could probably be more readily approached by examining patterns of variation in clutch size on a spatial scale, particularly in situations where wetland managers have experimental control over water-levels (e.g., Murkin and Kadlec 1986*b*).

Abundance of aquatic vegetation almost certainly increases throughout the nesting season in Northern Prairie wetlands (Krecker 1939, Polsini and Boyd 1972, Anderson 1975, Neckles 1984, McCrady et al. 1986), although nutritional quality is perhaps declining concurrently (Polsini and Boyd 1972, Neckles 1984). Likewise, most studies indicate that aquatic invertebrates are also increasing during the period when coots are producing eggs, although declines sometimes occur during the brood-rearing period (Baldassare 1978, DuBowy 1980, Gray 1980, Brown 1981, Diiro 1982, Murkin 1983, Neckles 1984, Wrubleski 1984, LaPointe 1986). Furthermore, the ingesta mass of collected adult coots increases seasonally throughout the breeding season (Table 5.1; declines during incubation probably reflect time of day when birds were collected, most incubating birds were collected at night). Collectively, these observations suggest that food is not the ultimate factor selecting for a seasonal decline in clutch size among coots (my supplemental feeding experiments, reported above and discussed below, suggest that food is not the proximate cause of the decline either).

Daan *et al.* (1988; see also Klomp 1970, Murphy 1986*b*) reviewed the phenomenon of seasonally declining clutch size among birds in general and concluded that it was not related to food availability for the egg-laying female or the nestlings. They suggested that reduced prospects of nest success, fledging success, and post-fledging survival later in the season select for lowered reproductive investment (see also Daan *et al.* 1990). Though not explicitly stated (Daan *et al.* 1988), this hypothesis assumes that significant costs are incurred by adult females that attempt a larger clutch (see Daan et al. 1990, Dijkstra et al. 1990). This hypothesis also implies that birds would be better off if they nested earlier, and begs the question "Why don't they?". Price *et al.* (1988) presented a population genetics model showing that there could be pronounced heritable variation in laying date within a population despite a strong correlation between laying date and fitness, provided that selection acted only on environmental variation (see also Alatalo *et al.* 1990, Cooke et al. 1990). They suggested that this environmental variation resulted primarily from variation in nutritional status of the laying female. Most supplemental feeding experiments have demonstrated significant advances in laying date among fed birds (reviewed in Martin 1987, Arcese and Smith 1988, Boutin 1990, Meijer et al. 1990), thus supporting this hypothesis, but my results with American Coots suggest that this hypothesis, at the very least, lacks universality.

3.4.3 *Trade-off between egg size and clutch size.*

Overall, there was a significant correlation between egg size and clutch size within the Minnedosa coot population, but this correlation was positive. Numerous other empirical studies have demonstrated positive correlations between avian life-history traits that are theoretically presumed to exhibit negative trade-offs (Smith 1981, 1988; Fitzpatrick and Woolfenden 1988; McCleery and Perrins 1988; Rohwer 1988; van Noordwijk and van Balen 1988; Rohwer and Eisenhauer 1989). One explanation for these unexpected positive correlations suggests that birds vary substantially in the quality of their territories, and that individuals on quality territories have more resources available for all aspects of their life cycles (e.g., Smith 1981, Högstedt 1981, Nur 1988*b*). Such inter-individual variation in resource holding potential is an important reason for conducting manipulative experiments to examine life-history trade-offs (Reznick 1985, Lessells 1986, Daan et al. 1990, Tinbergen and Daan 1990).

By providing supplemental food to large groups of coots, I experimentally provided them with high quality territories, and yet relationships between clutch and egg size were not affected in any consistent way (although relationships did vary significantly among sample groups). Through egg-removal experiments I was able to alter the clutch size of at least some females, but the ability of females to produce additional eggs was independent of previous egg size, and subsequent egg size was independent of how many eggs were eventually laid (coots laying additional eggs actually produced relatively larger final eggs). Similar results were obtained from egg-removal experiments involving Herring Gulls (*Larus* *argentatus*), Glaucous-winged Gulls (*L. glaucesenes*), Pied-billed Grebes (*Podilymbus podiceps*), and Horned Grebes (*Podiceps auritus*) (Parsons 1976; Fugle and Rothstein 1977; Reid 1987*a*; Arnold 1990, *unpubl. data*). Finally, by removing entire coot clutches, I was able to force females to produce many more eggs than they would normally have laid, but there was no evidence of a negative relationship between total eggs laid and egg size (in fact, there was a nearly significant positive correlation).

Based on these results, I conclude that female American Coots are not subjected to an allocational trade-off between clutch and egg size. I agree with Rohwer (1988, see also Rohwer and Eisenhauer 1989), who argued that this trade-off should be evident if clutch size is constrained by the ability of females to produce eggs (sensu Lack 1967, Ryder 1970, Ankney and Afton 1988). This lack of trade-off between clutch size and egg size has been observed in a wide variety of precocial birds with self-feeding young (Hepp *et al.* 1987, Rohwer 1988 [and 17 references therein], Lessells *et al.* 1989, Rohwer and Eisenhauer 1989, Schmutz and Braun 1989). Oddly, such trade-offs appear to be rather prevalent among altricial birds with parentally-fed young (N. E. Langston, pers. comm.), for which clutch size is not generally thought to be constrained by egg-laying capabilities (Lack 1947a, Ankney and Scott 1980, Krementz and Ankney 1986; but see references in Murphy and Haukioja 1986). I regard these data as weak evidence against the egg formation hypothesis.

3.4.4 *Effects of supplemental feeding on laying date, clutch size, and egg size.*

Coots receiving supplemental food tended to nest earlier than did unfed controls, but this effect was statistically significant only in 1987, or when data from all 3 years were combined. The overall effect size in the combined analysis averaged approximately 1 day in nesting seasons that spanned up to 46 days. Based on these data, I reject Perrin's (1970) hypothesis that timing of breeding is constrained by the amount of food available for the laying female; at most, food supply had a minor influence on laying date. This analysis does not imply that timing of breeding would be unaffected by drastic reductions in food supply, but it suggests that during three field seasons and in numerous individual wetlands, substantial variation in timing of breeding by individual coots was determined almost entirely by factors other than food availability.

Earlier laying by food-supplemented birds has been a common result in avian feeding studies (reviewed in Martin 1987, Arcese and Smith 1988, Boutin 1990; see also Meijer et al. 1988, 1990; Korpimäki 1989; Dhindsa and Boag 1990; Hörnfeldt and Eklund 1990). Thus, the meagre magnitude of the supplemental feeding effect in my study was somewhat surprising. However, most supplemental feeding experiments have involved bird populations that are year-round residents (e.g., Boutin 1990). In migratory species, such as American Coots, there may be less capacity to advance timing of breeding, although the latest nesting coot pairs did not seem to respond to supplemental food either; i.e., there was no effect of supplemental food on variance in laying date. It would be interesting to replicate Arcese and Smith's (1988) feeding experiments with "Vancouver" Song Sparrows (*Melospiza melodia*), or Ewald and Rohwer's (1982) work on "Seattle" Red-winged Blackbirds (*Agelaius phoeniceus*), in more seasonal environments like the Prairie Provinces. Both studies advanced laying by about 2 - 3 weeks among food-supplemented pairs (Ewald and Rohwer 1982, Arcese and Smith 1988), but such pronounced advances seem rather unlikely for prairie Canada.

Clutch size of coots increased with supplemental food in two of three years (1987 and 1988). In 1987, this increase could be attributed to a high "lipid" diet (supplemental corn) as opposed to a high protein diet (supplemental trout chow), although this may have only reflected differential palatability of the two food types. Although increased clutch size of supplementally-fed coots was consistent with the egg-formation hypothesis (especially the lipid limitation hypothesis; e.g., Ankney and Afton 1988), it was also consistent with the hypothesis that individual coots adjusted their clutch size based on the number of offspring they could successfully rear (the individual-optimization hypothesis; e.g., Högstedt 1980, Loman 1980). According to this hypothesis, supplemental feeding may have caused individual coots to assess the environment as being particularly good for raising young, and they therefore produced larger clutches in anticipation of future food abundance.

Conceptually, these two hypotheses could be contrasted using an experimental design that included both food supplementation and brood manipulations. By the future food abundance hypothesis (i.e., individual optimization), supplementally-fed parents would be able to raise all of their eggs to fledging only if food was provided throughout the brood-rearing period; removal of food after egg laying would result in increased nestling mortality. A corroborative experiment would involve providing pairs that did not receive supplemental food during laying with additional nestlings and food during the brood-rearing period; by the future food abundance hypothesis, parents could successfully raise these additional nestlings by making use of the food supplements. According to the egg formation hypothesis, birds receiving supplemental food during laying would be able to lay more eggs than unfed birds, and they would also be able to raise all of these eggs to fledging stage if food were removed after the end of egg laying. The corroborative experiment for this hypothesis would be to provide unfed parents with additional nestlings; by the egg formation hypothesis, they would be able to raise them, but by the future food abundance hypothesis they would not. However, given that the effect size in my feeding experiments was only about one egg (or less), it would probably be next to impossible to obtain the necessary quantity and quality of data to critically test these predictions.

Although supplemental food affected clutch size, it did not affect the nature of the relationship between clutch size and laying date. Seasonal declines in clutch size were of the same magnitude among fed and control coots, suggesting that the proximate (and ultimate?) cause of this decline was not food related. My results therefore differed markedly from most other supplemental-feeding experiments. Typically, supplementally-fed birds have initiated nesting earlier than controls, but have not altered their clutch or egg size (reviewed by Arcese and Smith 1988, Daan *et al.* 1988, Boutin 1990). In studies where clutch size was affected by supplemental food, it could often be attributed to a correlated response with earlier laying date (e.g., Högstedt 1981, Dijkstra *et al.* 1982, Meijer *et al.* 1988; but see Newton and Marquiss 1981, Arcese and Smith 1988, Hörnfeldt and Eklund 1990). Based on the relatively small sample sizes of fed individuals in many supplemental feeding studies (e.g., Poole 1985, Hochachka and Boag 1987, Hill 1988), I suspect that many previous feeding experiments lacked the statistical power necessary to detect differences in clutch size of the magnitude documented in my study (but see Hörnfeldt and Eklund 1990).

Egg size was not affected by supplemental feeding, suggesting that this trait is relatively inflexible in coots. My results thus differed substantially from those of Hill (1984, 1988), who suggested that in eastern Washington, American Coots altered egg size, rather than clutch size, in response to variation in resource availability. I suspect that Hill's conclusions were erroneous, especially in light of her sample sizes (i.e., only 3 food-supplemented territories). Moreover, results from other supplemental feeding studies are almost universal in suggesting that egg size is unaffected by proximal variation in food supply (Högstedt 1981; Poole 1985; Hochachka and Boag 1987; Arcese and Smith 1988; Korpimäka 1989; N. E. Langston and S. Rohwer, *pers. comm.*; T. W. Arnold, *unpubl. data*; but see Karlsson *in* Slagsvold *et al.* 1984, Reid 1987*a*), whereas clutch size often (though certainly not invariably) increases (see references in previous paragraph). However, it is interesting to note that, of 10 American Coot populations for which I could locate egg size data, average egg size was largest in three Pacific Northwest studies, including Hill's (Table 3.12). This suggests that Pacific Northwest coots may be under different selection pressures, and might therefore exhibit "crossing reaction norms" (sensu Stearns 1989) in response to resource variation. However, before concluding that there are crossing reaction norms lurking in the gene pool, or that the life-history strategy of Pacific Northwestern coots differs so fundamentally from that of most other birds, I would like to see Hill's feeding experiment replicated on a larger scale.

Table 3.12. Geographic variation in clutch size and egg size of the American Coot. Studies are listed in order of descending egg volume.

Location:	Sample Sizes[a] n_1	n_2	n_3	Mean Clutch Size	Mean Egg Volume	Source
Washington	41	4	30	6.71	29.68[b]	Fitzner et al. 1980
Washington	103	<145	888	7.91	28.35	Hill 1984
British Columbia	268	268	485	8.06	28.31	B. E. Lyon, pers. comm.
California	13	9	49	8.0	27.88	Gullion 1954
Manitoba, MDSA	383	619	~4000	9.6	27.84	This study
Hawaii	33	.	146	4.9	27.81	Byrd et al. 1985
Manitoba, Delta	136	149	~700	6.6	27.22	Arnold, unpubl. data
Iowa	85	.	407	7.9	27.05	Crawford 1975
Saskatchewan	69	.	168	8.57	26.97	Sutherland 1984
Wisconsin	380	432	2673	6.3	26.72	Bett 1983

Note: mean clutch size and mean egg size are uncorrelated ($r = 0.03$).

[a] Sample sizes: n_1 = number of nests for clutch size, n_2 = number of nests for egg volume, n_3 = number of eggs for egg volume.

[b] Volume calculated from relationship with egg mass. Some eggs were weighed during incubation, so volume likely underestimated due to water loss during incubation (e.g., Rahn and Ar 1974).

3.4.5 *Among wetland variation in laying date, clutch size, and egg size.*

Casual observations suggested that individual wetlands at Minnedosa exhibited considerable variation in abundance and/or species composition of submerged vascular plants and aquatic macroinvertebrates (e.g., Anderson and Jones 1976, Wrubleski 1984, Murkin and Kadlec 1986*a*). Presumably, such variation would translate into differential food availability for nesting coots. Other factors potentially important in regulating coot reproduction also varied among wetlands. Many wetlands were still partially covered by ice when coots arrived in the spring, which may have affected settlement chronologies. Residual emergent vegetation was greatly reduced by wind, ice, or fire on some wetlands, which may have caused coots to delay nesting until new growth provided substrate for nest attachment and concealment. Intraspecific strife may have varied among wetlands, which may have forced some birds to invest more heavily in territorial defense. In most years, timing of breeding was more synchronous among pairs nesting on the same wetland than could be expected by chance. In contrast, clutch size was similarly influenced in only two of six years and egg size was unaffected by wetland variation. Although one explanation for the laying date effect is that timing of breeding varied in parallel with chronology of food abundance among wetlands, the preceding results with supplemental food make this hypothesis somewhat tenuous. I suspect that variation in timing of breeding among wetlands may have been related to among-wetland variation in settlement chronologies, social conflict (or facilitation) among pairs, or quality of nesting cover.

During two years, Hill (1988) documented significant variation in laying date, clutch size, and egg size of American Coots among four wetland basins differing significantly in resource quality, as assayed by water conductivity, insect emergence, and ratios of Yellow-headed (*Xanthocephalus xanthocephalus*) to Red-winged blackbirds. Egg size varied in parallel with wetland quality, whereas clutch size and laying date did not. Hill once again considered this to be evidence that coots adjust egg size, rather than clutch size, in response to variation in food availability, and once again, these results are in direct conflict with my findings.

Bett (1983) examined habitat-related variation in breeding success of coots on a large marsh in Wisconsin by comparing reproductive attributes among three major and 11 minor vegetation zones (like me, he did not attempt to directly measure food abundance). Bett found significant differences in laying date, clutch size, and egg size among vegetation zones (the egg size relationship was improperly analyzed, because individual eggs within clutches were treated as statistically independent), and similarly to my results, he found that laying date, clutch size, and egg size varied in concert. However, Bett (1983) made no attempt to partition this covariance to determine if clutch and egg size relationships were being driven by variation in laying date.

3.4.6 *Variation in laying rates.*

Coots exhibited significantly fewer laying skips when they were provided with supplemental food. This suggests that on at least some days, some individual coots encountered difficulty in meeting the nutritional demands of egg formation. Other authors have also suggested that long laying intervals (< 1 egg per d) are caused by difficulties in obtaining sufficient food for egg formation (Lack 1968, Astheimer 1985), but these conclusions were based on interspecific comparisons, many involving very large birds that produce very large eggs. I am not aware of any other study that has demonstrated significant within-population variation in laying rates in relation to food availability. Lack and Lack (1951) suggested such a relationship for European Swifts (*Apus apus*), but Lack was unusually quick to attribute most differences in reproductive behavior to food availability. Newton and Marquiss (1984) documented slower laying rates among Eurasian Sparrowhawks (*Accipiter nisus*) late in the nesting season, but did not imply that it was food related. One alternative explanation for my results, that supplementally-fed coots were more likely to interrupt normal laying to lay eggs parasitically in other coots' nests, was not supported by patterns of parasitic egg-laying; coots adopting a mixed strategy of laying both normal and parasitic eggs appeared to lay parasitically before initiating a clutch of their own (Lyon *in press*;

Arnold *unpubl. data*). Another alternative explanation, that some coots use laying skips to increase the degree of hatching asynchrony, requires that asynchronous broods could fledge more offspring under conditions of less-abundant (or less predictable) food. Both the brood-reduction hypothesis (Lack 1947*a*) and the peak-load reduction hypothesis (Hussell 1972) could satisfy these requirements, but these hypotheses have not withstood critical testing (Amundsen and Stokland 1988, Mock and Schwagmeyer 1990).

In 1990 (the only year with sufficient renesting data), laying rates were significantly lower among renesters, as predicted for prairie dabbling ducks (*Anas* spp.) by Afton and Ankney (1988) according to the egg formation ("lipid limitation") hypothesis. I caution that my data are based on 3 of 22 renesters that exhibited multiple laying skips, in comparison to 2 of 41 initial nesters that had single laying skips. In spite of these sample size concerns, I suspect that this is probably a biologically real difference. Strohmeyer (1967) also recorded a higher incidence of laying skips among renesting, as opposed to first-nesting, Blue-winged Teal (*Anas discors*) (skip-rates = 0.045 and 0.022, n = 89 and 358 exposure days, respectively), but this difference was not significant (Fisher's exact test, 1 tailed, P = 0.20).

Thus, my data on laying rates of supplementally-fed and renesting coots provide general support for the egg formation hypothesis, at least among some fraction of the population. However, this fraction is undeniably small ($\leq$ 10%).

3.4.7 *Egg-removal experiments.*

During three of four years (1985, 1986, and 1988; but not 1987), coots laid larger clutches when six eggs were experimentally removed from their nests during egg laying. When variation due to laying date was statistically controlled, annual variation in experimental response to egg-removal was statistically significant. Thus, the lack of response in 1987 was not a statistical anomaly; in fact, this year had the most removal data.

Although removal coots often laid more total eggs than did controls, they did not, on average, replace all six eggs that had been removed. Removal birds laid 1 more egg than did controls, and hence their nests contained 5 fewer eggs, on average, at clutch completion. There appeared to be pronounced individual variation in response to egg removals, some coots produced supernormal clutches (i.e., ≥ 16 eggs), whereas others laid as few as 5 eggs. This was reflected in measures of variability, in all 4 cases where mean clutch size increased, the variance also increased (though not significantly so, except in an overall analysis).

Results from the egg-removal experiments provided mixed support for the egg-formation hypothesis. Some birds clearly responded to the removals by laying more eggs than they normally would have laid, but most coots appeared unable or unwilling to replace the six eggs that had been removed. These results are similar to most other studies on determinacy of egg-laying in precocial and semi-precocial birds, in which birds failed to respond to egg-removals, or only responded in part (McAllister 1958, Barry 1962, Parsons 1976, Fugle and Rothstein 1977, Rohwer 1984, Reid 1987*a*, Arnold 1990). When interpreting these studies, however, the distinction between being unable and unwilling to continue laying becomes crucial (Klomp 1970, Rohwer 1986*c*). Daily egg-removals are designed to fool a laying female into "thinking" she has laid fewer eggs than she actually has, but some females might be recognizing these removals and interpreting them as partial clutch predation. If such were the case, the adaptive response might be to abandon the current nest and begin a new nest elsewhere (Armstrong and Robertson 1988). Proximate physiological mechanisms of clutch-size determination (and when these occur) need to be better understood in order to properly interpret egg-removal experiments (e.g., Meijer et al. 1990). If clutch size (i.e., total eggs to be laid) is determined at the time the first egg is laid, then egg-removal cannot affect final clutch size, regardless of whether or not clutch size is limited by the ability of females to form eggs (Klomp 1970, Briggs 1985). Unfortunately, very little is known about these proximate mechanisms. Rohwer (1986*c*) suggested that investigators might find a way out of this proximate/ultimate conundrum by studying continuation nesting. Fortunately, coots were very amenable to such research.

3.4.8 *Renests and continuation nests.*

Approximately 80% of destroyed coot nests were replaced by subsequent nesting attempts. Most of the nests that were not replaced were destroyed very late in the nesting season; thus, coots may have some kind of seasonal "giving-up point", after which renesting is no longer profitable. Measures of past reproductive investment such as number of previous nests, clutch size, and egg size did not influence the propensity to renest. There was, however, a nearly significant effect of incubation stage on renesting propensity; coots were less likely to renest if their clutches were destroyed late in incubation. This effect may have been due to the relationship between stage of incubation and renesting intervals. For nests destroyed during laying or on the first day of incubation, renests were usually initiated after only a 0 to 4 day interval, but nests destroyed after day 2 of incubation were not replaced for 4 to 7 days. Hence, coots losing their nests during incubation faced longer renesting delays than did coots losing their nests during laying, and the prospect of this delay might have lowered the expected benefits of renesting to such a point that, for some birds, it may not have been profitable to renest.

Renesting intervals were related to several factors in addition to incubation stage. Nests destroyed late in the breeding season required longer to replace, on average, but this did not seem to be a function of past investment in egg formation, because there were no inhibitory effects of number of previous nesting attempts, previous clutch size, or previous egg size on the renesting interval. In fact, renesting intervals were significantly shorter for those coots that had laid the most previous clutches, a result that I refuse to interpret too literally. Renesting intervals also tended to be shortest among coots that produced the largest renest clutches (this effect was independent of laying date effects).

For a variety of multi-brooded passerine birds, renesting propensity, renesting intervals, renesting clutch size, and renesting fledging success have been negatively affected by the amount of parental investment devoted to the previous brood (McGillivray 1983, Hegner and Wingfield 1987, Smith *et al.* 1987, Tinbergen 1987, Slagsvold and Lifjeld 1989). The lack of relationships among renesting propensity, renesting interval, number of previous clutches, previous clutch size, and previous egg size suggest that extended egg production in American Coots does not entail any measureable reproductive costs.

Although effects of previous incubation on renesting propensity and renesting intervals might seem to imply a reproductive cost, I believe there is a more consistent explanation for these patterns. If the physical stress of incubation itself were important, then renesting intervals should continue to increase monotonically with number of days incubated, but this does not occur (Fig. 3.5). The increase occurs only during the first 5 days of incubation, and is probably related to natural regression of the ovary and oviduct following clutch completion. Dry mass of the oviduct ranges from 4 - 6 g among laying coots, but it declines exponentially to about 0.5 g during the first 5 days of incubation (Appendix 6). Similarly, any large follicles remaining in the oviduct after clutch completion become atretic, whereby most nutrients are resorbed by the body. Hence, a female that loses her nest during laying will likely have another large follicle ready for immediate egg production (unless she is about to lay her last egg), and a female one or two days postlaying may have a large follicle available that has not yet gone atretic, but a female several days postlaying will have to initiate follicle development from scratch, because incubating birds do not maintain follicles in preparation for potential renesting (Arnold *pers. obs.*). Laying females with continuous follicular hierarchies (i.e., females that were likely to continue laying several more eggs) had from 3 to 6 developing follicles (see Chapter 5 for definitions), implying that individual eggs are formed in 4 to 7 days (1 d for albumen and shell deposition) (see also Alisauskas and Ankney 1985, who estimated a slightly longer period of 8 d). Hence, based on these considerations, it seems that most coots are renesting as fast as is physiologically possible.

It is unfortunate that this experiment was not conducted in conjunction with supplemental feeding. Although I am convinced that my preceding arguments on physiological limitations account for most of the observed variation in renesting intervals among coots, my arguments would be stronger if supplemental food had no detectable influence on renesting propensity or renesting intervals. Swanson *et al.* (1986) studied renesting among captive Mallards (*Anas platyrhynchos*) in "semi-natural" pond inclosures, and found that food availability influenced renesting intervals and renest clutch sizes, but not renesting propensity. All Mallards with access to supplemental food renested within 5 to 10 d of clutch removal, a slightly longer period than what I observed among coots (Mallards probably take a day or two longer to develop follicles; see Ankney and Afton [1988] for the closely related Northern Shoveler [*Anas clypeata*]).

Although I believe that my data on renesting propensity and renesting intervals provide a strong rejection of the hypothesis that nutrient reserves limit clutch size among American Coots (*contra* Alisauskas and Ankney 1985), curiously, I also believe that they provide some general support for this hypothesis as it applies to temperate-nesting ducks. Ducks of the genus *Bucephala* (i.e., Buffleheads [*B. albeola*] and goldeneyes) do not generally renest (Gauthier 1989, Zicus 1990), although they would seem to have adequate time available to do so. In waterfowl species that do renest, renesting intervals increase with time spent incubating the previous clutch, beyond what could be expected from simple regression of the ovary and oviduct (Fig. 3.6). Because most waterfowl use nutrient reserves during incubation (as evidenced by mass loss and/or carcass analysis; e.g., Afton and Paulus, *in press*), the positive correlation between renesting interval and time spent incubating the previous clutch suggests a causal role of nutrient reserves. Moreover, the variation in renesting intervals is much higher among ducks than among coots (Fig. 3.6), suggesting that physiological constraints associated with regression of the ovary and oviduct are an insufficient explanation of renesting delays among most ducks. The necessity of repairing could have increased the renest intervals of some individual ducks (i.e., most ducks are serially monogamous with no male parental care), but typically, renesting hens remate with their previous drake (Strohmeyer 1967, Humburg *et al.* 1978, Anderson 1985). Nest predation rates are substantially higher on upland nesting ducks than on over-water nesting coots (ca. 12% nest

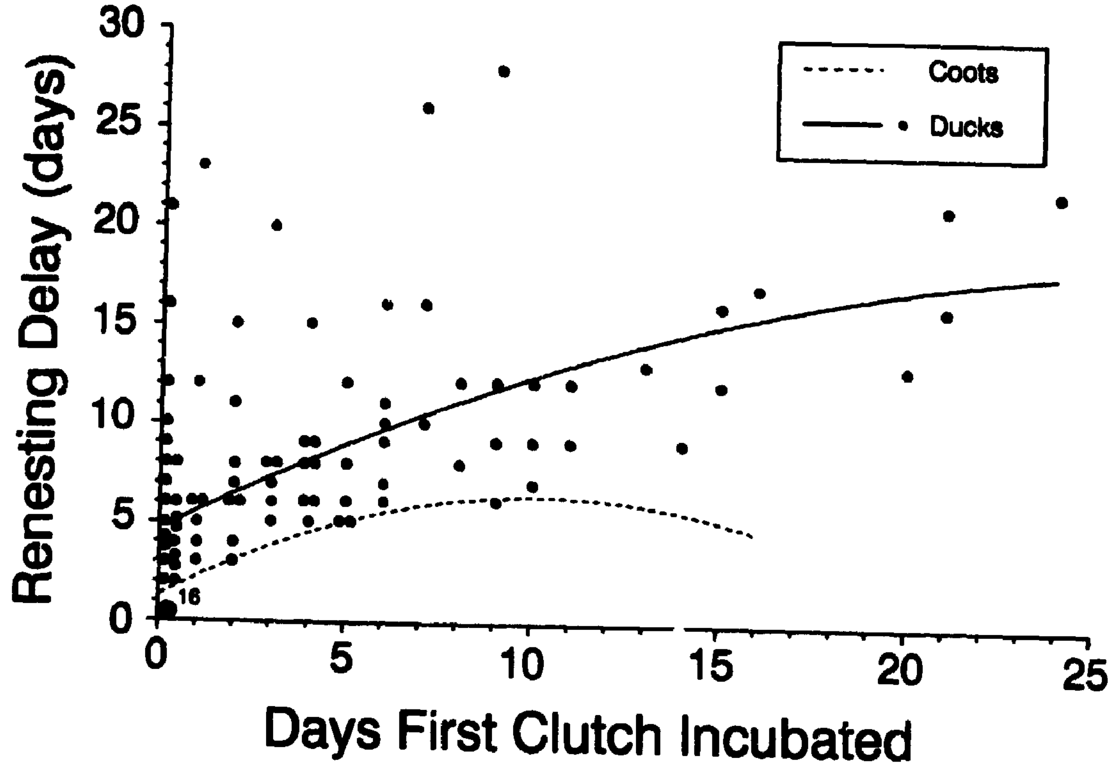


Fig. 3.6. Renesting delay of prairie-nesting ducks in relation to the number of days the previous clutch had been incubated on the day of clutch destruction (day 0 = nests destroyed during laying). Each point represents one renesting attempt, except the large point at 0, 0 which represents 16 nests. Out of 100 renests, 80 lie above the regression line for American Coots (the dashed line) and 38 exceed 8 days (the maximum time required to form an egg from an undeveloped ova). Duck data are from *Anas acuta, A. platyrhynchos, A. strepera, A. clypeata, A. discors, Aythya valisineria, A. americana,* and *Oxyura jamaicensis* (Sowls 1955, Gates 1962, Strohmeyer 1967, Alliston 1979, Doty *et al.* 1984, Duncan 1987*a*, Tome 1986).

success in *Anas* spp., *vs.* 80% in coots; Arnold *et al.* 1987, Arnold *unpubl. data*), so if anything, ducks should have been exposed to stronger selection for rapid renesting capability. Understanding this difference in speed of renesting between ducks and coots will involve more than documenting their patterns of nutrient reserve use during incubation and their renesting characteristics. Ideally, such research would involve supplemental feeding (e.g., Swanson *et al.* 1986) and determination of nutrient reserve dynamics of renesting females (e.g., Rohwer 1986*a*). Until such critical tests of the egg-formation hypothesis are conducted for temperate-nesting ducks, all that can be safely concluded is that nutrient reserves invariably decline during egg laying (e.g., Ankney and Alisauskas *in press*).

The renesting data provided no support for the hypothesis that seasonally declining clutch size is a function of increased numbers of renests as the season progresses. Although renest clutch size did decline seasonally, it declined in parallel with first nest clutch size. There was even a nonsignificant trend for renest clutch size to be larger than initial nest clutch size at any given laying date. I suspect that this was a function of individual covariation in clutch size and laying date, i.e., some birds were consistently "superior" to other birds, and these superior birds, on average, nested earlier and produced larger clutches than "inferior" birds. But if superior birds were forced to renest at a later date, so that the timing of their renest clutches were in synchrony with the first nesting attempts of inferior birds, they still tended to lay more eggs than the inferior birds. This was evidenced by nearly significant repeatability for clutch size among renesting birds (r_i = 22%, P = 0.10), and fairly high repeatability for relative clutch size (i.e., clutch size corrected for population-level covariation with laying date: r_i = 39%, P = 0.009). Because these repeatability estimates are only cross-seasonal, and females remained with the same mate (in all but one case, see Appendix 4) and on the same territory between nesting attempts, these individual consistencies in clutch size need not reflect genetic differences among females, but they nevertheless might. Once again, it would be instructive to do renesting experiments in conjunction with supplemental feeding. By getting renesting data from supplementally-fed females and from unfed females, and additional data from females with access to supplemental food for their first clutch but not their renest clutch (and *vice versa* for other females), it may be possible to partition out effects of territory quality and effects of female quality (which may or may not be genetic).

I am aware of four other studies that compared clutch sizes of initial and renest clutches while controlling for laying date. Duncan (1987*a*) found no difference in clutch size with nesting attempt among captive Northern Pintails (*Anas acuta*), and Alliston (1979) found no difference among wild-nesting Redheads (renest clutches appeared to be larger than initial clutches initiated on the same date, but there was little distributional overlap in the two groups). Newton and Marquiss (1984) and Hochachka (1990) found that renesting (and/or double-brooding) Eurasian Sparrowhawks and Song Sparrows produced larger clutches than did other females that were producing initial clutches at the same time. Collectively, these studies support the hypothesis that covariation in clutch size and laying date is due largely to variation in female quality. In support of this hypothesis, Slagsvold and Lifjeld (1988, 1990) showed, by experimentally altering female quality among Pied Flycatchers (*Ficedula hypoleuca*) and 3 tit (*Parus*) species (selected wing and tail feathers were removed to reduce flight efficiency), that renest clutch size was primarily affected by female quality (level of handicapping).

Several coots in the renesting experiment produced absolutely phenomenal numbers of sequential or near-sequential eggs (e.g., 35/37 d, 34/39 d, 27/28 d, 23/24 d, 21/22 d; Appendix 4). Most of these birds were eventually successful in hatching a clutch (Appendix 4), suggesting that there were no insurmountable costs associated with this extensive egg laying. I believe that these data, in and of themselves, are sufficient to refute the egg formation hypothesis as a viable explanation of clutch-size limitation in American Coots. Scott and Ankney (1980) used a similar argument, and data on rapid renesting by Gray Catbirds (*Dumetella carolinensis*) and Northern Cardinals (*Cardinalis cardinalis*) (Scott *et al.* 1987), to suggest that female passerines generally are not limited by their ability to procure nutrients for egg laying. Rohwer (1986*c*) has summarized several anecdotal records of continuous laying among dabbling ducks, although additional studies of this phenomenon are clearly needed to critically test the egg-formation hypothesis for temperate-nesting waterfowl.

CHAPTER 4. SOURCES OF VARIATION IN THE COMPOSITION OF AMERICAN COOT EGGS

4.1 INTRODUCTION

Egg size has been positively correlated with several likely components of offspring fitness (see Section 3.1). These benefits are usually attributed to greater quantities and/or proportions of nutrients (i.e., fat and protein) present in large versus small eggs (Ankney 1980, Alisauskas 1986), because such benefits would not likely exist if large eggs simply contained more water than did small eggs. Greater water content might be adaptive for desert or oceanic birds (e.g., Ricklefs et al. 1978), but the majority of birds, including coots, are probably not constrained by water availability. In most studies, egg size has been a good predictor of nutrient composition (Ankney 1980, Ankney and Johnson 1985, Alisauskas 1986, Murphy 1986*a*, Rohwer 1986*b*, Muma and Ankney 1987). But in some birds, variation in egg size has been primarily due to water content, and thus, egg size has been a rather poor predictor of nutrient content (Ricklefs 1984*b*, Arnold 1989). It is therefore important to test the assumption that large eggs contain more nutrients than small eggs before speculating on the possible adaptive value of egg size in a particular population.

I know of no studies that have examined the heritability of egg composition among wild birds, but heritabilities have ranged from 0.18 to 0.61 for albumen and shell characteristics among inbred lines of domestic chickens (Hill *et al.* 1966, Washburn 1979). Within-clutch repeatabilities for egg composition among wild birds are often as high as for egg size (e.g., Ricklefs 1984*b*, Alisauskas 1986, Rohwer 1986*b*, Hepp *et al.* 1987, Arnold 1989), and egg size is usually highly heritable (reviewed in Lessells *et al.* 1989). These observations suggest that egg composition might also be highly heritable among wild birds, and therefore relatively insensitive to environmental variation. However, if birds can alter the nutritional content of their eggs, and if this can occur without affecting egg size, then studies relying solely on egg size information (such as my analyses in Chapter 3) are clearly inappropriate for testing allocational trade-offs among breeding birds.

Although food supply has been shown to affect a number of reproductive characteristics in birds (see Chapter 3; general review in Martin 1987, Boutin 1990), its influence on egg composition has been largely ignored, with the exception of domestic birds (but see Hochachka 1988). Animal scientists, working primarily with chickens, have demonstrated some flexibility in egg composition with respect to diet quality (Fisher 1969, Begin and Insko 1972, Butts and Cunningham 1972). Among chickens, however, eggs are "optimized" with respect to economic efficiency and human palatability, rather than embryo viability. Thus, although feeding experiments with captive birds may illustrate plasticity of egg composition, they shed little light on the adaptive basis for such changes.

Alisauskas (1986) demonstrated that most variation in egg composition of American Coots occurred among, rather than within, clutches, although repeatabilities were somewhat lower for yolk components than for whole egg, shell, and albumen components (see also Ricklefs 1984*b*, Rohwer 1986*b*, Arnold 1989). These data suggest an inherent effect of either the laying female (including such factors as genetics, age, nutrient reserves) or her territory (proximate food availability) on egg composition.

In this chapter, I assess several potential sources of proximate variation in the composition of American Coot eggs. I begin by examining annual variation over three years (1987-89) that ranged from extremely dry (1989) to fairly wet (1987). In each year, subsamples of coots were provided with supplemental food, and I test for effects of this high-quality food resource on egg composition. I obtained data for two or more eggs from several wetlands, and I use these data to assess among-wetland variation in egg composition. Finally, I examine variation in egg composition with respect to clutch size and laying date. These analyses are therefore identical to many of those in Chapter 3, except that egg size has been replaced by various measures of nutrient composition. In the next chapter (5), I assess the effects of some inherent qualities of the female (e.g., age, body size, and nutrient reserves) on egg size and composition. Because I did not determine egg composition of related kin, or of individual females over time, I cannot assess heritability and repeatability with my data.

4.2 METHODS

4.2.1. *Field work.*

The study area, years of study, and supplemental feeding methods are described in Sections 2.2 and 2.3, and nest searching is described in Section 3.2. In 1987, 1988, and 1989, supplemental feeding began 10, 15, and 8 days before the first freshly-laid eggs were collected for nutrient analysis, and 20, 22, and 19 days before the mean egg collection dates, respectively. Coots require 5 - 8 days to produce an egg (including 4 - 7 days of rapid follicle growth and 1 day of albumen and shell synthesis, Appendix 6; see also Alisauskas and Ankney 1985), so most coots had adequate time to respond to supplemental food prior to egg formation.

From a subsample of each year's nests, I collected a single fresh (i.e., < 24 hr old) egg per nest for nutrient analysis. Previously laid eggs were identified by visiting nests one day before the collection day and marking all eggs. I attempted to standardize potential effects of egg sequence (e.g., Alisauskas 1986) by collecting fifth-laid eggs within each clutch; however, this was not always logistically feasible, in which case I collected eggs as near in sequence as possible to the fifth-laid egg. To avoid affecting clutch size through egg-removal (which in retrospect was unlikely; see Section 3.3.7), I replaced collected eggs with an egg obtained from off the study area. For each collected egg, I determined length, maximum breadth, and fresh mass (± 0.1 g). Eggs were then boiled for 5-10 minutes, individually bagged in plastic, and frozen for up to 4 months.

4.2.2. *Laboratory analyses.*

In the laboratory, eggs were separated into yolk, albumen, and shell (membranes were removed from the shell and included with the albumen;

Alisauskas 1986). Wet components were dried at 80°C for > 48 hr to obtain dry component masses (Kerr *et al.* 1982). Most eggs lost considerable water ($\bar{X}$ = 1.9 g) during processing (i.e., from boiling, freezing, and handling; see also Ricklefs 1982, 1984*b*), and more importantly, the amount of water loss varied significantly among sample groups (ANOVA: $F_{(7,225)} = 8.57$, $P = 0.0001$). Because water loss varied among groups, I did not analyze wet component masses; however, total water content could be accurately assessed by subtracting dry component masses from fresh egg mass. Dry yolks were further analyzed to determine lipid (yolk-fat) and nonlipid (yolk-lean) fractions. Neutral lipids were extracted from dried yolks by refluxing the entire yolk for 4 hr in a modified Soxhlet apparatus using petroleum ether as solvent (Dobush *et al.* 1985). Dry albumen and yolk-lean were assumed to consist entirely of protein (Sotherland and Rahn 1987). Nutrient composition of each egg was calculated as follows: fat (g) = yolk-fat; protein (g) = dry albumen + yolk-lean; and energy (kcal) = 9.5 * fat + 5.65 * protein (Ricklefs 1984*b*).

4.2.3 *Statistical analyses.*

Data were obtained from eight sample groups of eggs; these included four feeding groups in 1987 (M87CTRL, M87TROUT, M87CORN, and M87C+T), two in 1988 (M88CTRL and M88MIX), and two in 1989 (M89CTRL and M89MIX). I tested for among-group differences in variance using F_{max} tests (Sokal and Rohlf 1973: 210), and for among group diffences in means using one-way ANOVAs. Proportional differences in egg composition were examined using $\log_{10}$-$\log_{10}$ regressions of component masses versus egg mass. I tested for year and supplemental-feeding effects by including appropriate dummy variables and interaction terms in the regression models (i.e., ANCOVAs). I examined among-group homogeneity of variance in proportional egg composition by conducting F_{max} tests on residuals from the common regression of $\log_{10}$ egg component mass on $\log_{10}$ egg mass.

Because the egg composition data included such a large number of variables (8) and sample groups (8), I adopted the following statistical protocol to help minimize Type I errors: (1) A single multivariate test (MANOVA or MANCOVA) was conducted on all 8 variables across all 8 sample groups. (2) If the overall MANOVA or MANCOVA was significant, I used additional MANOVAs or MANCOVAs to test for two effects of specific interest: a) supplemental feeding effects, and b) year effects. Because feeding methods differed between 1987 and 1988-89, I could not do a combined analysis of feeding and year effects unless I could justify pooling data from the four 1987 treatments into two groups: "fed" and "control" (e.g., in Chapter 3, clutch size was influenced only by corn supplements, so I pooled 1987 data by ignoring trout chow; "fed" was synonymous with "corn-fed"). Hence, my first sublevel of analyses involved supplemental feeding effects in 1987, using a full factorial design of corn effects, trout chow effects, and corn * trout chow interaction effects. If this analysis justified pooling data among years, I would then procede to test for supplemental feeding effects, year effects, and interaction effects using the entire set of data. Otherwise, I would analyze feeding effects separately for each year, and annual effects only among control groups. (3) If MANOVAs or MANCOVAs were significant, I interpreted individual ANOVAs or ANCOVAs for each variable. (4) Finally, if ANOVAs or ANCOVAs were significant, I used Least Significant Difference (LSD) tests to examine specific differences among groups. Thus, I initially conducted only two statistical tests, and any additional tests were conditional upon the significance of the preceding tests. I believe that this approach was superior to that of adjusting experiment-wise error rates, because it provided powerful statistical tests at each step (my data included 672 potential pair-wise comparisons of mean, slope, and intercept, so to maintain $P < 0.05$ on an experiment-wise basis, P critical would have been 0.00007).

Similar protocols were adopted to test for variation in proportional egg composition with clutch size and laying date; these analyses included potential effects of clutch size, laying date, egg size, and sample group, as well as higher-order interactions among these variables.

I calculated among- and within-wetland variation in egg composition using nested-ANOVAs (SAS NESTED procedure, SAS Institute 1985), but because of an unbalanced statistical design, F tests were calculated using the GLM procedure. Nested-ANOVAs were conducted for each year separately, and for the three years combined (a few wetlands were included more than once in the combined analysis). Because supplemental food was allocated among wetlands, rather than among coot pairs, wetland effects were nested within supplemental feeding effects for these analyses. Most other statistical analyses were performed using the GLM procedure. For analyses involving more than one predictor variable (i.e., ANCOVAs), I deleted nonsignificant ($P > 0.05$, based on Type III SS) effects from the models and recalculated significance levels for the remaining variables. Significance levels for MANOVAs and MANCOVAs were based on the Wilk's Lambda approximation to the F distribution (SAS Institute Inc. 1985).

4.3 RESULTS

I obtained data on the nutrient composition of 235 eggs, with sample sizes ranging from 19 to 47 per group (Table 4.1). Two or more eggs were obtained from each of 52 wetlands during the three years (160 eggs total); data from these eggs were used in the analysis of among-wetland variation (Section 4.3.6).

Although I attempted to minimize sequence effects on egg composition by collecting the fifth-laid egg from each clutch, there were nevertheless significant differences in egg sequence among sample groups (ANOVA: $F_{(7,227)} = 3.58$, $P = 0.001$). This was primarily a function of many late-sequence eggs in the 1987 samples (Table 4.1). Because laying order can affect egg composition in coots (Alisauskas 1986), I tested for sequence effects on among-group variation in egg composition by repeating these analyses using egg sequence as a covariate (i.e., ANCOVA; Section 4.3.4). There was also significant variation in clutch size and laying date among groups (e.g., annual and supplemental feeding effects; Section 3.3.1 and 3.3.4), so if clutch size and laying date affected egg composition, they could also influence among-group differences.

Table 4.1. Sample size, laying sequence, estimated volume (cm^3), fresh mass (g), clutch size, and laying date of American Coot eggs used in composition analysis (values are X ± 1 SD).

Group[a]:	Sample Size	Laying Sequence	Estimated Volume	Fresh Mass	Clutch Size	Laying[b] Date
M87CTRL	24	5.8 ± 1.4	27.2 ± 2.7	29.1 ± 2.8	9.0 ± 1.6	137.3 ± 5.0
M87CORN	24	5.9 ± 2.2	28.3 ± 1.6	30.3 ± 1.8	10.5 ± 1.9	136.5 ± 5.4
M87TROUT	21	6.0 ± 1.6	28.4 ± 2.3	30.3 ± 2.4	9.9 ± 1.8	136.9 ± 5.5
M87C+T	24	5.8 ± 2.0	28.1 ± 2.5	29.9 ± 2.8	10.6 ± 1.8	135.7 ± 3.9
M88CTRL	42	5.2 ± 0.7	28.2 ± 2.2	30.1 ± 2.4	9.2 ± 2.1	139.9 ± 4.6
M88MIX	47	5.3 ± 0.8	28.1 ± 2.3	30.0 ± 2.3	10.2 ± 2.1	139.1 ± 3.4
M89CTRL	34	4.4 ± 2.2	27.8 ± 2.2	29.5 ± 2.5	8.9 ± 1.9	138.8 ± 4.6
M89MIX	19	4.8 ± 1.9	27.2 ± 2.4	28.9 ± 2.6	9.9 ± 3.1	140.6 ± 6.1
Combined	235	5.3 ± 1.6	28.0 ± 2.3	29.8 ± 2.5	9.7 ± 2.1	138.3 ± 4.9

[a] Sample group mnemonics: M designates Minnedosa Study Area, numerals designate year, terminal letters designate supplemental feeding regime (CTRL=unfed controls, CORN=corn, TROUT=trout chow, C+T= corn and trout chow, MIX=mixed diet of 1988 and 1989).

[b] Julian date.

4.3.1 *Among-group variation in egg composition.*

Means and variances of egg size variables (length, maximum breadth, estimated volume, and fresh mass) did not differ among sample groups (Table 4.1; ANOVAs, $P \geq 0.37$; F_{max} tests, $P \geq 0.05$), hence any of the among-group differences in egg quality described in the following analyses would not have been detected using only egg-size criteria.

Mean egg composition differed significantly among sample groups (MANOVA: $F_{(35,932)} = 3.59$, $P < 0.0001$). Total water, shell mass, and albumen mass were the only components that did not vary among groups (Table 4.2).

Given that egg size did not differ among sample groups, but that most measures of egg composition did, I logically expected that there would be significant differences in the proportional composition of coot eggs. There was no significant sample group * egg mass interaction effect (i.e., slopes from the regressions of egg component masses on total egg mass were essentially parallel; MANCOVA: $F_{(56,1147)} = 0.97$, $P = 0.56$). With this interaction effect removed, main effects of sample group and egg mass were both highly significant (i.e., component masses increased with egg mass, but different sample groups, on average, had different proportions of specific components; MANCOVA: group effect, $F_{(56,1185)} = 2.65$, $P < 0.0001$; egg mass effect, $F_{(8,219)} = 7.95 \times 10^5$, $P << 0.0001$). Individual ANCOVAs explained from 51 to 97% of the variation in measures of egg composition (Table 4.3). Effects of egg mass were highly significant for each ANCOVA ($P \leq 0.0001$), and group effects were significant for all variables except shell mass ($P = 0.78$).

Most components varied isometrically with egg mass (i.e., log-log regression slopes did not differ significantly from unity, thus component masses comprised a constant proportion of total egg mass). However, the log-log regression slope was significantly less than one for shell mass ($b = 0.90 \pm 0.05$ [1 SE]), and significantly greater than one for albumen mass ($b = 1.20 \pm 0.06$) and protein mass ($b = 1.12 \pm 0.04$). Because these components were not isometric, it would be inappropriate to use ratio variables to describe proportional egg composition among sample groups (Packard and Boardman 1988). I therefore

Table 4.2. Component masses (g) and energy content (kcal) of American Coot eggs (X ± SD).

Group:	Total Water	Egg Dry Mass	Shell Dry Mass	Albumen Dry Mass	Yolk Fat	Yolk Lean Dry	Protein Dry Mass	Total Energy
M87CTRL	19.9 ± 1.8	9.16 ± 1.06	2.64 ± 0.29	2.36 ± 0.34	2.63 ± 0.40	1.54 ± 0.24	3.89 ± 0.46	47.0 ± 6.0
M87CORN	20.6 ± 1.3	9.68 ± 0.61	2.75 ± 0.23	2.40 ± 0.24	2.83 ± 0.23	1.71 ± 0.15	4.10 ± 0.30	50.0 ± 3.2
M87TROUT	20.7 ± 1.7	9.54 ± 0.81	2.73 ± 0.34	2.37 ± 0.22	2.75 ± 0.32	1.68 ± 0.16	4.05 ± 0.29	49.1 ± 4.4
M87C+T	20.3 ± 2.0	9.52 ± 0.93	2.71 ± 0.34	2.39 ± 0.43	2.81 ± 0.29	1.61 ± 0.18	4.00 ± 0.50	49.3 ± 4.8
M88CTRL	20.9 ± 1.7	9.20 ± 0.79	2.68 ± 0.24	2.30 ± 0.26	2.60 ± 0.30	1.63 ± 0.17	3.93 ± 0.37	46.8 ± 4.5
M88MIX	20.7 ± 1.7	9.29 ± 0.82	2.68 ± 0.27	2.29 ± 0.27	2.65 ± 0.30	1.67 ± 0.22	3.95 ± 0.40	47.5 ± 4.5
M89CTRL	20.6 ± 1.7	8.93 ± 0.79	2.63 ± 0.24	2.21 ± 0.26	2.57 ± 0.33	1.51 ± 0.19	3.72 ± 0.36	45.5 ± 4.5
M89MIX	19.9 ± 1.8	8.95 ± 0.86	2.54 ± 0.16	2.20 ± 0.29	2.65 ± 0.37	1.56 ± 0.20	3.76 ± 0.42	46.4 ± 5.5
F_{max}	2.37	3.02	4.52	3.82	3.02	2.56	2.97	3.52
P^a	NS	NS	**	*	NS	NS	NS	*
F_{ANOVA}	1.20	2.60	1.37	1.80	2.53	3.95	3.02	3.06
P	0.30	0.01	0.22	0.09	0.02	0.0004	0.005	0.004

[a] *, $P < 0.05$; **, $P < 0.01$; NS, $P > 0.05$.

Table 4.3. Sources of variation in proportional composition of American Coot eggs[a].

	F_{max} test[b]		Egg size effect[c]			Group effect		Interaction		Model[d]	
Variable:	F_{max}	P	log(a)	b + SE(b)	F	F	P	F	P	F	r^2
Total water	1.96	NS	-0.15	0.99 ± 0.01	6040	7.70	0.0001	1.03	0.41	785.0	0.97
Egg dry mass	1.96	NS	-0.53	1.02 ± 0.03	1239	7.50	0.0001	1.04	0.40	170.2	0.86
Shell	4.00	**	-0.90	0.90 ± 0.05	275	0.58	0.78	0.94	0.48	294.3	0.56
Albumen	3.24	*	-1.40	1.20 ± 0.06	369	3.01	0.005	1.89	0.07	49.9	0.64
Yolk fat	1.65	NS	-1.05	1.00 ± 0.07	201	3.68	0.0009	1.74	0.10	29.3	0.51
Yolk lean	2.25	NS	-1.30	1.02 ± 0.07	184	3.55	0.001	1.23	0.29	29.6	0.51
Protein	3.06	NS	-1.06	1.12 ± 0.04	1022	6.66	0.0001	1.84	0.08	142.4	0.83
Energy	1.65	NS	0.13	1.05 ± 0.04	715	7.27	0.0001	1.72	0.11	100.5	0.78
MANCOVA	--		--	-- --	794514	2.65	0.0001	0.97	0.54	--	--

[a] N = 235 eggs, k = 8 groups.

[b] F_{max} tests based on variance of residuals from the common regression of log10 component mass on log10 egg mass.

[c] Egg size = fresh egg mass (g); $\log_{10}$(component mass) = log10(a) + b[log10(fresh egg mass)]. $P < 0.0001$ for all egg size effects.

[d] Model includes significant parameters only; $P < 0.0001$ for all models.

calculated proportional component masses (Table 4.4) using residuals from the common regressions (i.e., on all eggs) of component masses on egg mass (Table 4.3); these residuals were standardize to a fresh mass of 29.8 g (the grand mean for all 235 eggs). This was an appropriate way to express proportional composition, since slopes of component masses on egg mass were homogeneous in almost all cases. In the few instances where there were significant interaction effects involving egg size, individual regression lines were plotted (Figs. 4.1 and 4.2).

Variation in proportional egg composition was significantly heterogeneous for shell and albumen mass (Table 4.3), but within-group variance showed no obvious patterns with respect to supplemental feeding or year (Table 4.4).

4.3.2 *Effects of supplemental food on egg composition.*

For the 1987 data, there was a significant interaction effect involving corn and trout chow supplements (Table 4.5; MANOVA: P = 0.02). The only individual variable affected by this interaction was yolk-lean, but the effect on it was highly significant (P = 0.003). Yolk-lean was significantly higher among eggs laid by birds receiving either corn or trout chow, but not among birds receiving both supplements (Table 4.4; see also Fig. 4.1*b*). Main effects of corn and trout chow were not significant (MANOVAs: P > 0.43) (the ANOVA for corn effect on yolk-fat was individually significant, but this effect was ignored based on MANOVA criterion).

Proportional composition was affected by the three-way interaction among egg mass, corn, and trout chow was also significant (Table 4.5; MANCOVA: P = 0.02); however, this effect was individually significant only for protein content (P = 0.02). Because visual inspection of the plotted regression lines did not reveal any interpretable relationship (see Fig. 4.1*a*), I deleted the three-way interaction and fit a reduced model to these data. For most variables, corn effects were significant (Table 4.5: albumen content, yolk-fat, yolk-lean, protein, and total energy), but yolk-lean was also affected by trout chow and the interaction between corn and trout chow (Fig. 4.1*b*). Corn-fed birds produced small eggs of

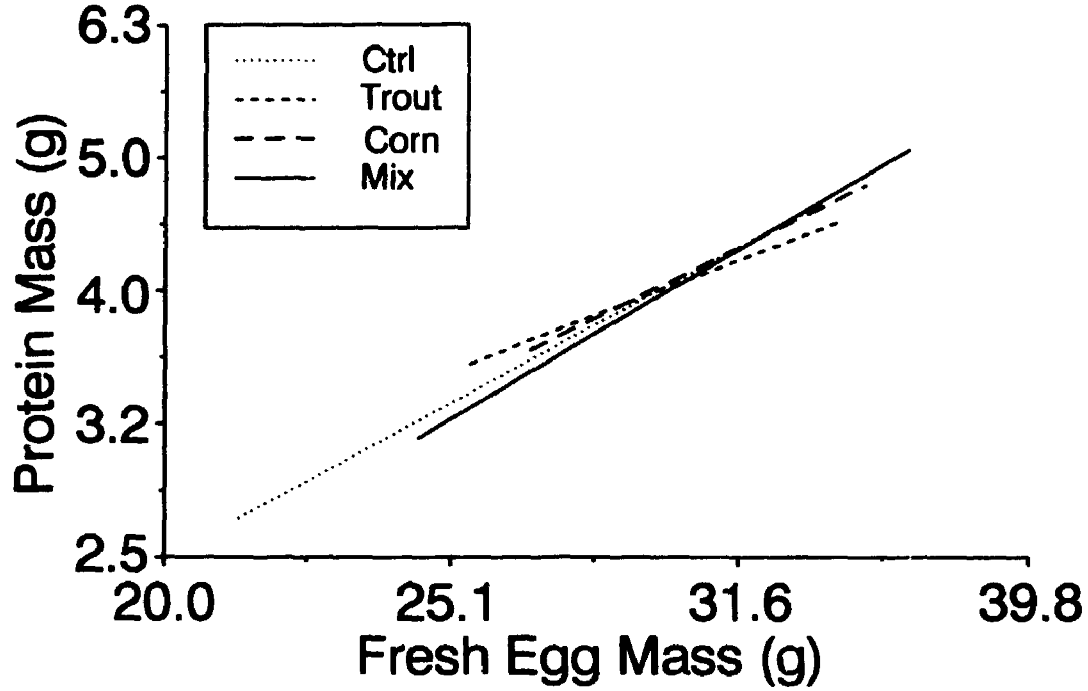
Table 4.4. Proportional composition (percent of fresh egg mass)[a] and energy content (kcal/g fresh egg mass) of American Coot eggs (values are X ± SD).

	Percent Composition							
Group:	Total Water	Egg Dry Mass	Shell Dry Mass	Albumen Dry Mass	Yolk Fat	Yolk Lean	Protein Dry Mass	Energy Content
M87CTRL	68.5 ± 1.2	31.5 ± 1.2	9.0 ± 0.5	8.2 ± 0.9	9.0 ± 0.8	5.3 ± 0.6	13.4 ± 0.7	1.62 ± 0.08
M87CORN	68.0 ± 1.0	32.0 ± 1.0	9.1 ± 0.5	7.9 ± 0.5	9.3 ± 0.7	5.6 ± 0.4	13.5 ± 0.4	1.65 ± 0.07
M87TROUT	68.5 ± 1.0	31.5 ± 1.0	9.0 ± 0.8	7.8 ± 0.5	9.1 ± 0.8	5.6 ± 0.4	13.4 ± 0.4	1.62 ± 0.08
M87C+T	68.1 ± 1.1	31.9 ± 1.1	9.1 ± 0.8	8.0 ± 0.9	9.4 ± 0.9	5.4 ± 0.5	13.4 ± 0.7	1.65 ± 0.08
M88CTRL	69.3 ± 1.0	30.6 ± 1.0	8.9 ± 0.5	7.6 ± 0.5	8.6 ± 0.7	5.4 ± 0.4	13.0 ± 0.6	1.56 ± 0.07
M88MIX	69.0 ± 1.4	30.9 ± 1.4	8.9 ± 0.7	7.6 ± 0.6	8.8 ± 0.8	5.5 ± 0.6	13.1 ± 0.6	1.58 ± 0.08
M89CTRL	69.5 ± 1.1	30.4 ± 1.1	9.0 ± 0.5	7.6 ± 0.7	8.8 ± 0.8	5.1 ± 0.5	12.7 ± 0.6	1.55 ± 0.08
M89MIX	69.0 ± 1.0	31.0 ± 1.0	8.8 ± 0.4	7.7 ± 0.6	9.2 ± 0.9	5.4 ± 0.4	13.0 ± 0.4	1.61 ± 0.09

[a] Proportional composition based on residuals from regressions of component mass on fresh egg mass (Table 4.3); standardized to fresh egg mass = 29.8 (the grand mean for all eggs).

Table 4.5. Effects of supplemental food on absolute and proportional egg composition of American Coots in 1987.

		Absolute Composition			Proportional Egg Composition (ES significant in all models; P < 0.0001)							
Variable:		Corn	Trout	C*T	Corn	Trout	C*T	C*ES	T*ES	C*T*ES	Model	(r^2)
Total water	F	0.25	0.64	2.22	3.59	0.31	0.01	3.33	1.10	1.59	2603.46	
	P	0.62	0.43	0.14	0.06	0.58	0.93	0.07	0.30	0.21	0.0001	(0.97)
Egg dry mass	F	2.12	0.32	2.12	3.57	0.31	0.00	3.46	1.21	1.77	638.89	
	P	0.15	0.58	0.15	0.06	0.58	0.95	0.07	0.27	0.19	0.0001	(0.88)
Shell	F	0.73	0.19	1.05	0.12	0.17	0.06	0.30	0.05	0.45	130.31	
	P	0.40	0.67	0.31	0.74	0.68	0.80	0.59	0.83	0.50	0.0001	(0.59)
Albumen	F	0.22	0.01	0.02	7.52	0.30	1.54	7.44	0.01	2.28	55.45	(0.65)
	P	0.66	0.94	0.90	0.007	0.58	0.22	0.008	0.91	0.14	0.0001	
Yolk fat	F	3.79	0.58	1.17	11.93	0.00	0.03	11.56	0.95	0.78	41.02	(0.58)
	P	0.05	0.45	0.28	0.0008	0.95	0.86	0.001	0.33	0.38	0.0001	
Yolk lean	F	9.76	6.62	1.17	7.77	4.70	7.62	1.02	3.35	0.53	21.50	(0.49)
	P	0.002	0.01	0.003	0.007	0.03	0.007	0.32	0.07	0.47	0.0001	
Protein	F	0.98	0.09	2.33	0.34	5.07	5.67	0.33	5.08	5.62	72.46	(0.86)
	P	0.32	0.77	0.13	0.56	0.03	0.02	0.57	0.03	0.02	0.0001	
Energy	F	2.94	0.39	2.04	6.29	0.09	0.00	6.02	1.92	3.06	120.96	(0.80)
	P	0.09	0.53	0.16	0.01	0.76	1.00	0.02	0.17	0.08	0.0001	
MANOVA	F	0.99	0.30	2.87	1.99	1.97	2.43	1.98	1.96	2.42	--	
	P	0.43	0.91	0.02	0.06	0.06	0.02	0.06	0.06	0.02	--	



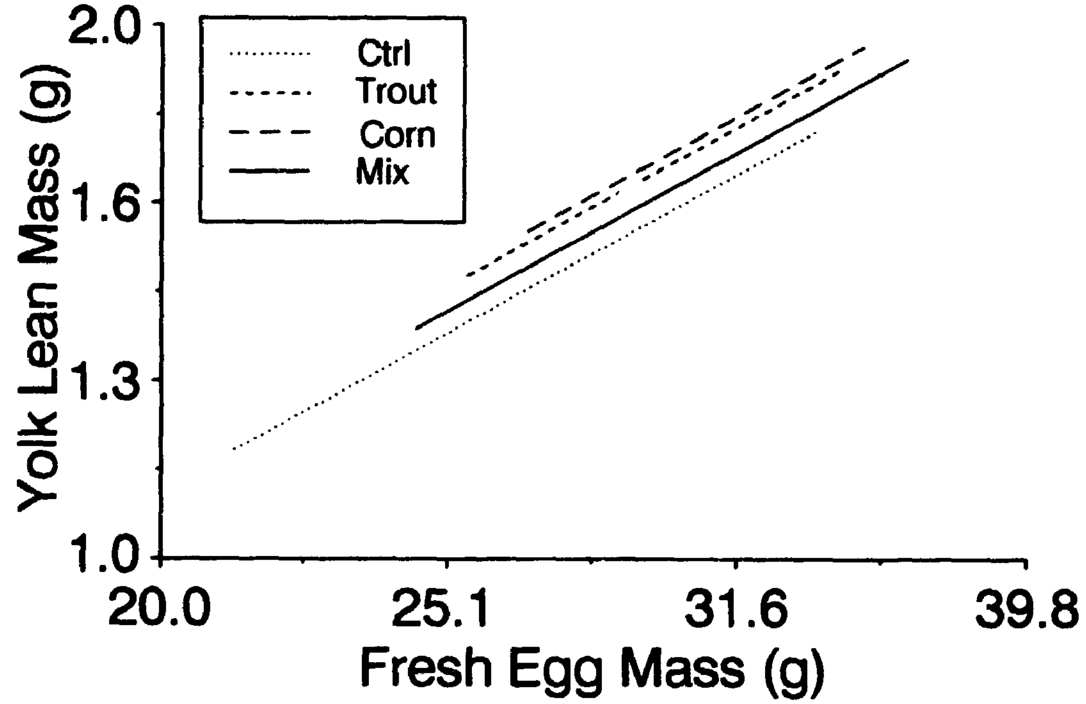


Fig. 4.1. Top: interaction effect of different supplemental food types on protein content of American Coot eggs in 1987. This "effect" was ignored. Bottom: Effect of supplemental food on lean yolk mass in 1987. This "effect", though interpretable, was not very intuitive.

greater lipid and energy content, but large eggs were not more nutrient rich than control eggs (Fig. 4.2). Albumen content was lower among small eggs of corn-fed birds (Fig. 4.2).

Because there was evidence that trout chow interacted with corn to affect some aspects of egg composition in 1987, I did not pool the data by year for combined statistical analysis.

Supplemental feeding did not affect either absolute or proportional egg composition in 1988 (Table 4.6). In 1989, the MANOVA indicated a significant feeding effect on absolute composition, but this effect was not obvious for any single variable (Table 4.6), nor could I find evidence of significant differences in covariances among albumen, yolk-fat, and yolk-lean, or between dry mass and total water. For proportional composition in 1989, the MANCOVA for feeding effect was suggestive ($P = 0.09$), and individual effects were significant or nearly significant for water, drymass, yolk-lean, protein, and energy (Table 4.6). Eggs from fed birds contained more nutrients, and less water, than did control eggs (Table 4.4; see also Fig. 4.3).

4.3.3 *Annual variation in egg composition.*

Annual variation in absolute egg composition was highly significant (Table 4.7; MANOVA: $P < 0.0001$ [control groups only]), but this effect was individually significant only for yolk-lean (Table 4.7; $P = 0.02$). There were highly significant annual differences, however, in the pattern of covariance between yolk-fat and yolk-lean (ANCOVA: $P = 0.009$). In 1988, the correlation between these two variables was much weaker ($r^2 = 0.30$) than during 1987 and 1989 ($r^2 = 0.78$ and 0.68, respectively). This same general pattern was apparent among eggs from supplementally-fed coots (1987: $r^2 = 0.46$, 1988: $r^2 = 0.26$, 1989: $r^2 = 0.80$).

Annual variation in proportional composition was also highly significant (Table 4.7; MANCOVA: $P = 0.0001$), and in this case affected all variables except shell mass ($P = 0.68$) and yolk-fat ($P = 0.10$). Relative fat, protein, and energy content were highest in 1987, and lowest in 1989 (Table 4.4; see also Fig. 4.3).

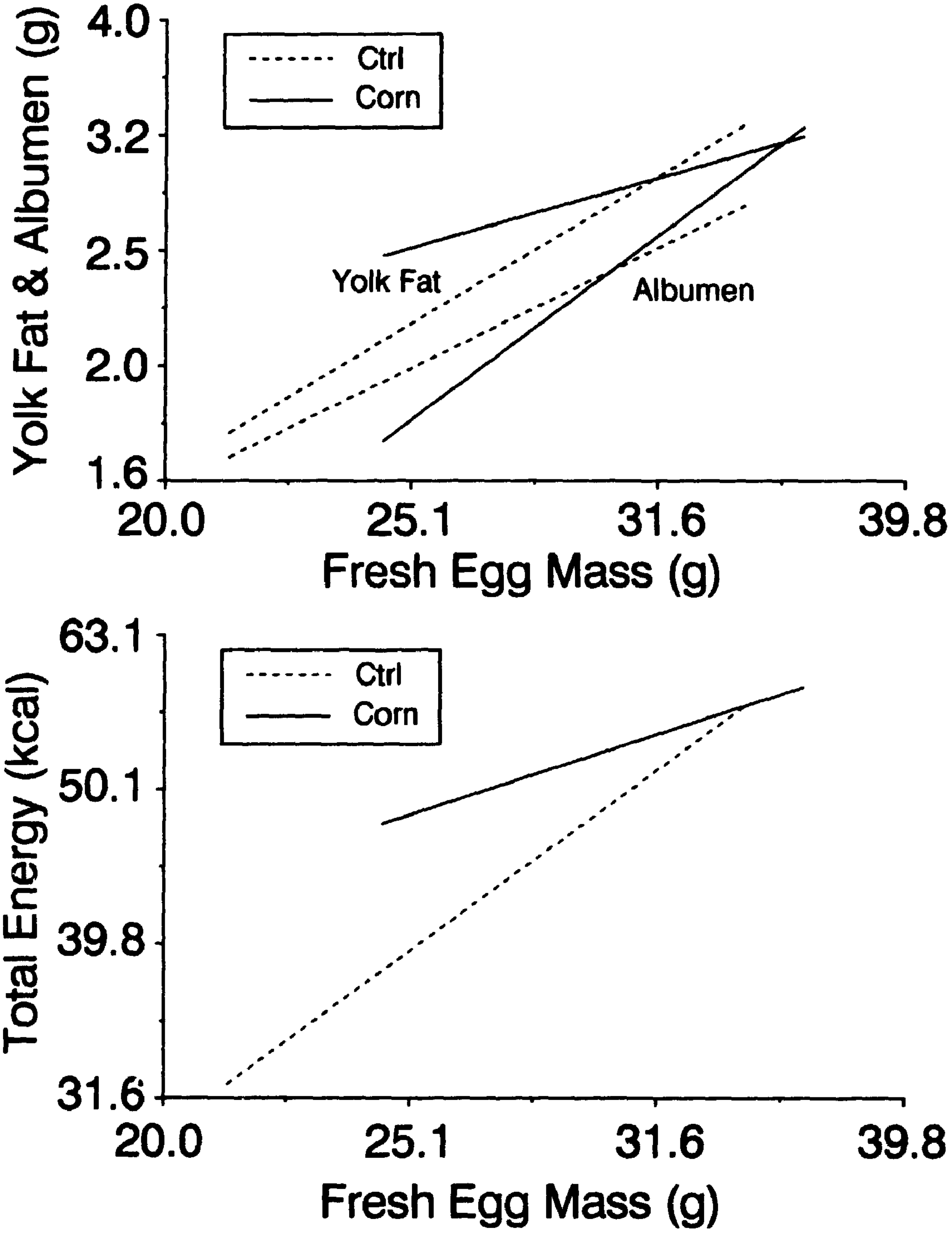


Fig. 4.2. Top and bottom: Effects of corn supplements on proportional yolk fat, albumen, and energy content of American Coot eggs in 1987. Ctrl (controls) includes birds receiving supplemental trout chow; corn includes some birds receiving both corn and trout chow.

Table 4.6. Effects of supplemental food on absolute and proportional egg composition of American Coots in 1988 and 1989.

	Absolute		Proportional				Absolute		Proportional			
	1988 Food		1988 Food		1988 Food*ES[a]		1989 Food		1989 Food		1989 Food*ES[a]	
Variable:	F	P	F	P	F	P	F	P	F	P	F	P
Water	0.11	0.75	1.57	0.21	0.01	0.91	0.89	0.35	3.39	0.07	0.28	0.60
Egg dry mass	0.25	0.62	1.34	0.25	0.02	0.90	0.01	0.92	3.42	0.07	0.26	0.61
Shell	0.00	0.98	0.00	0.99	0.03	0.85	2.41	0.13	2.35	0.13	4.43	0.04
Albumen	0.03	0.85	0.08	0.77	0.00	0.96	0.03	0.87	0.18	0.67	0.71	0.40
Yolk fat	0.85	0.36	1.58	0.21	0.27	0.60	0.67	0.42	2.68	0.11	0.45	0.50
Yolk lean	0.70	0.40	0.94	0.33	2.23	0.14	0.80	0.37	3.78	0.06	0.27	0.61
Protein	0.09	0.76	0.44	0.51	1.43	0.23	0.12	0.73	4.84	0.03	2.46	0.12
Energy	0.55	0.46	2.33	0.13	0.00	1.00	0.49	0.49	5.78	0.02	1.56	0.22
MANOVA	0.54	0.75	1.41	0.20	0.53	0.83	2.66	0.03	1.88	0.09	1.72	0.12

[a] Egg size (ES) include as main effect in proportional models; it was always highly significant ($P < 0.0001$).

Table 4.7. Annual variation in absolute and proportional egg composition of unfed American Coots, 1987 - 1989.

	Absolute		Proportional Composition			
	Year effect		Year effect		Year*ES[a]	
Variable:	F	P	F	P	F	P
Water	2.27	0.11	7.97	0.0006	3.44	0.04
Egg dry mass	1.05	0.35	7.68	0.0008	3.46	0.04
Shell	0.45	0.64	0.38	0.68	0.37	0.69
Albumen	1.96	0.15	6.03	0.003	0.50	0.61
Yolk fat	0.21	0.81	2.33	0.10	1.81	0.17
Yolk lean	4.11	0.02	3.60	0.03	1.25	0.29
Protein	2.88	0.06	9.83	0.0001	0.96	0.39
Energy	0.97	0.38	5.93	0.004	3.05	0.05
MANOVA	4.80	0.0001	3.42	0.0001	0.85	0.62

[a] ES = Egg size (fresh mass). Main effect of egg size was also included in the model; it was significant for all components ($P < 0.0001$).

4.3.4 *Effects of laying sequence on egg composition.*

Egg composition was somewhat affected by laying sequence (MANCOVA: $F_{(10,298)} = 2.11$, $P = 0.06$; group effect included in model), but sequence effects were small and were not significant for any individual component ($P > 0.17$). Adjusting for sequence effects did not appreciably alter the significance or magnitude of differences among sample groups.

Laying sequence affected proportional egg composition (MANCOVA: $F_{(8,218)} = 3.11$, $P = 0.02$), but this effect approached significance only for albumen mass (partial $r^2 = 0.006$, $P = 0.06$) and yolk-lean (partial $r^2 = 0.007$, $P = 0.08$). Albumen mass increased marginally with laying sequence, whereas yolk-lean declined in an opposite fashion; hence, total-protein did not vary with laying sequence. Correcting for laying sequence did not affect the significance or magnitude of previously described differences in proportional egg composition among sample groups.

4.3.5 *Effects of clutch size and laying date on egg composition.*

Egg composition was affected by clutch size (MREG: $F_{(5,180)} = 8.13$, $P < 0.0001$, $n = 186$ eggs; sample size is reduced because not all eggs in previous analyses were from clutches that survived until laying was completed and clutch size could be determined), with all components increasing significantly with clutch size. Egg composition was also affected by laying date (MREG: $F_{(5,226)} = 5.35$, $P < 0.0001$), with all components except total water declining significantly with laying date. Clutch size effects remained significant when sample group was included in the analysis, and group effects also remained significant (MANCOVA: P(*CS*) < 0.0001, P(*GROUP*) < 0.0001), but there was no significant interaction between these two factors (P(*CS*GROUP*) = 0.10). Similar results were obtained with laying date and sample group (MANCOVA: P(*DATE*) = 0.003, P(*GROUP*) = 0.0001, P(*DATE*GROUP*) = 0.19). When clutch size and laying date were analyzed jointly, both factors had significant influences on overall egg composition, but date effects were weak (MREG: P(*CS*) = 0.0002, P(*DATE*) = 0.05). Clutch size effects remained significant for all variables, but laying date effects were individually significant only for yolk-lean (P = 0.02), protein (P = 0.05), and total energy (P = 0.04) (they were nearly significant for dry mass [P = 0.07] and yolk-fat [P = 0.09]). There was no interaction between clutch size and laying date (MREG: $F_{(5,176)}$ = 1.42, P = 0.22; with sample group included in model: $F_{(5,169)}$ = 0.75, P = 0.59).

Proportional egg composition varied with clutch size (MREG: $F_{(8,176)}$ = 4.09, P = 0.0002), with dry mass, yolk-fat, yolk-lean, protein, and energy all increasing with clutch size, and water content decreasing. The interaction between egg size and clutch size was marginally significant (MREG: $F_{(8,175)}$ = 1.86, P = 0.07); in relatively large clutches, relatively large eggs contained relatively more water (P = 0.02) and relatively less dry mass, yolk-fat, and energy (P = 0.02, 0.03, and 0.05, respectively). Proportional composition also varied with laying date (MREG: $F_{(8,222)}$ = 3.05, P = 0.003), with proportions of dry mass, yolk-fat, yolk-lean, protein, and energy all declining seasonally, and water content increasing. Interaction effects with the covariate, fresh egg mass, were not significant (MREG: $F_{(8,221)}$ = 0.89, P = 0.52; individual P's ≥ 0.11). Clutch size and laying date effects remained significant when both variables were analyzed jointly (MREG: P(*CS*) = 0.01, P(*DATE*) = 0.05), with most components (except water) increasing with clutch size and declining with laying date. Effects of clutch size and laying date also remained significant when sample group was included in this analysis (MANCOVA: P(*CS*) = 0.02, P(*DATE*) = 0.05, P(*GROUP*) = 0.0001).

4.3.6 *Among-wetland variation in egg composition.*

There was no significant among-wetland variation in absolute or proportional egg composition in any year, or for the three years combined (Table 4.8; P ≥ 0.07, % Var. ≤ 23.1, k = 48 comparisons).

Table 4.8. Among-wetland variation in absolute (ABS) and proportional (PROP) egg composition of American Coots[a].

Variable:	1987-ABS		1987-PROP		1988-ABS		1988-PROP		1989-ABS		1989-PROP		ALL DATA-ABS		ALL DATA-PROP	
	r_i	P	r_i	P	r_i	P	r_i	P	r_i	P	r_i	P	r_i	P	r_i	P
Water	0.0	0.54	0.0	0.51	9.0	0.30	13.6	0.20	5.4	0.28	0.0	0.74	2.2	0.37	4.2	0.26
Egg dry mass	0.0	0.53	0.0	0.52	0.0	0.53	13.6	0.20	9.2	0.23	0.0	0.75	0.4	0.46	4.4	0.26
Shell	0.0	0.60	0.0	0.59	11.2	0.26	23.1	0.10	1.2	0.53	0.7	0.44	0.3	0.51	7.2	0.20
Albumen	0.0	0.77	0.0	0.84	9.8	0.29	0.0	0.93	0.0	0.44	4.2	0.36	0.0	0.64	0.0	0.93
Yolk fat	1.8	0.43	0.0	0.79	0.0	0.52	8.0	0.32	11.4	0.19	0.0	0.67	3.0	0.34	0.0	0.71
Yolk lean	0.0	0.76	0.0	0.86	0.0	0.93	0.0	0.53	1.5	0.39	0.0	0.82	0.0	0.90	0.0	0.87
Protein	0.0	0.60	13.6	0.15	0.0	0.53	0.0	0.61	7.3	0.26	16.1	0.07	0.0	0.53	7.6	0.12
Energy	3.3	0.38	1.4	0.43	0.0	0.53	9.1	0.28	10.5	0.20	0.0	0.90	3.1	0.33	0.0	0.50

[a] Results from nested-ANOVAs (PROC NESTED; SAS Institute Inc. 1985); r_i is the intraclass correlation coefficient. P values calculated with PROC GLM. Analyses based on proportional composition used residuals from common regression of component mass on total egg mass.

4.4 DISCUSSION

Overall trends in absolute and proportional egg composition in this study were generally as described by Alisauskas (1986) for American Coots nesting at Delta Marsh, Manitoba. However, Alisauskas concluded that yolk components and total energy comprised a relatively larger fraction of egg contents among large eggs (i.e., positive allometry), whereas albumen comprised a relatively smaller fraction of total egg contents (negative allometry). I found that dry albumen was positively allometric, dry shell was negatively allometric (as predicted based on interspecific relationships between surface area and volume, and between shell thickness and egg size; e.g., Ar et al. 1974), and all other components were isometric (i.e., no relative change with egg size). Because Alisauskas' (1986) results were not verified in other samples of eggs from Delta Marsh (Arnold, Alisauskas, and Ankney *in revision*), I attribute his results either to Type I statistical error, or to an effect involving among- and within-clutch variation (Hochachka 1986, Rohwer 1986*b*, R. T. Alisauskas *pers. comm.*).

There appears to be no discernable pattern among bird species with respect to which egg components show positive allometry, which display isometry, and which exhibit negative allometry. Alisauskas (1986) reviewed data on proportional egg composition in relation to egg size and mode of development (i.e., altricial *vs.* precocial) and found no pattern; additional data sets have largely upheld that conclusion (e.g., Bancroft 1984, Hill 1984, Shaw 1985, Hochachka 1986, Murphy 1986*a*, Rohwer 1986, Hepp et al. 1987, Meathrel and Ryder 1987, Meathrel et al. 1987, Muma and Ankney 1987, Owen and West 1988, Arnold 1989, Arnold, *unpubl. data*). Regardless, all studies to date have demonstrated that larger eggs contain larger absolute amounts of at least one essential nutrient (i.e., fat or protein), even among species where most variation in egg mass is attributable to relative water content (Ricklefs 1984*b*, Arnold 1989).

4.4.1 *Among-group variation in egg composition.*

Analyses of both absolute and proportional egg composition revealed highly significant among-group variation. However, most of this variation was not associated with interpretable effects (e.g., supplemental feeding and annual variation; Fig. 4.3; but see ensuing discussions).

4.4.2 *Effects of supplemental food on egg composition.*

Overall, supplemental feeding had very little effect on egg composition. For some statistically significant interaction effects in the 1987 experiment, it was difficult to attribute any biological relevance to the observed patterns. "Interpretable" effects in 1987 included an interaction effect of corn and trout chow on absolute size of the yolk-lean fraction, and effects of corn on the proportional content of yolk fat, albumen, and energy in small eggs. It is not known what relevance the yolk lean fraction has in determining embryo viability (but see next section). The effects of supplemental corn on proportional composition suggested that nutrient content of eggs might be proximately influenced by availability of dietary lipids, but only among those birds laying small eggs (the converse interpretation, that corn-fed birds increased egg size without similarly increasing yolk lipid, was not supported by data on egg size variation in relation to supplemental feeding; Chapter 3).

In 1988, with the largest annual data set, I detected no differences in either absolute or proportional egg composition with respect to supplemental feeding.

In 1989, the MANOVA suggested a significant effect of feeding on absolute egg composition, but no single variable was significantly affected. Nor could I find any evidence of significantly different patterns of covariation among components (i.e., trade-offs among albumen, yolk-fat, and yolk-lean, or between water content and dry mass). When I controlled for variation in egg size, feeding effects were nearly significant for the MANCOVA ($P < 0.10$), and individually significant for protein and energy content (and nearly significant for water, dry mass, and yolk-lean).

There was a consistent trend for supplementally-fed birds to have more yolk-fat in their eggs (Fig. 4.3). This was also apparent in data from 1989 from Delta Marsh, Manitoba (Arnold, Alisauskas, and Ankney *in revision*). Overall,

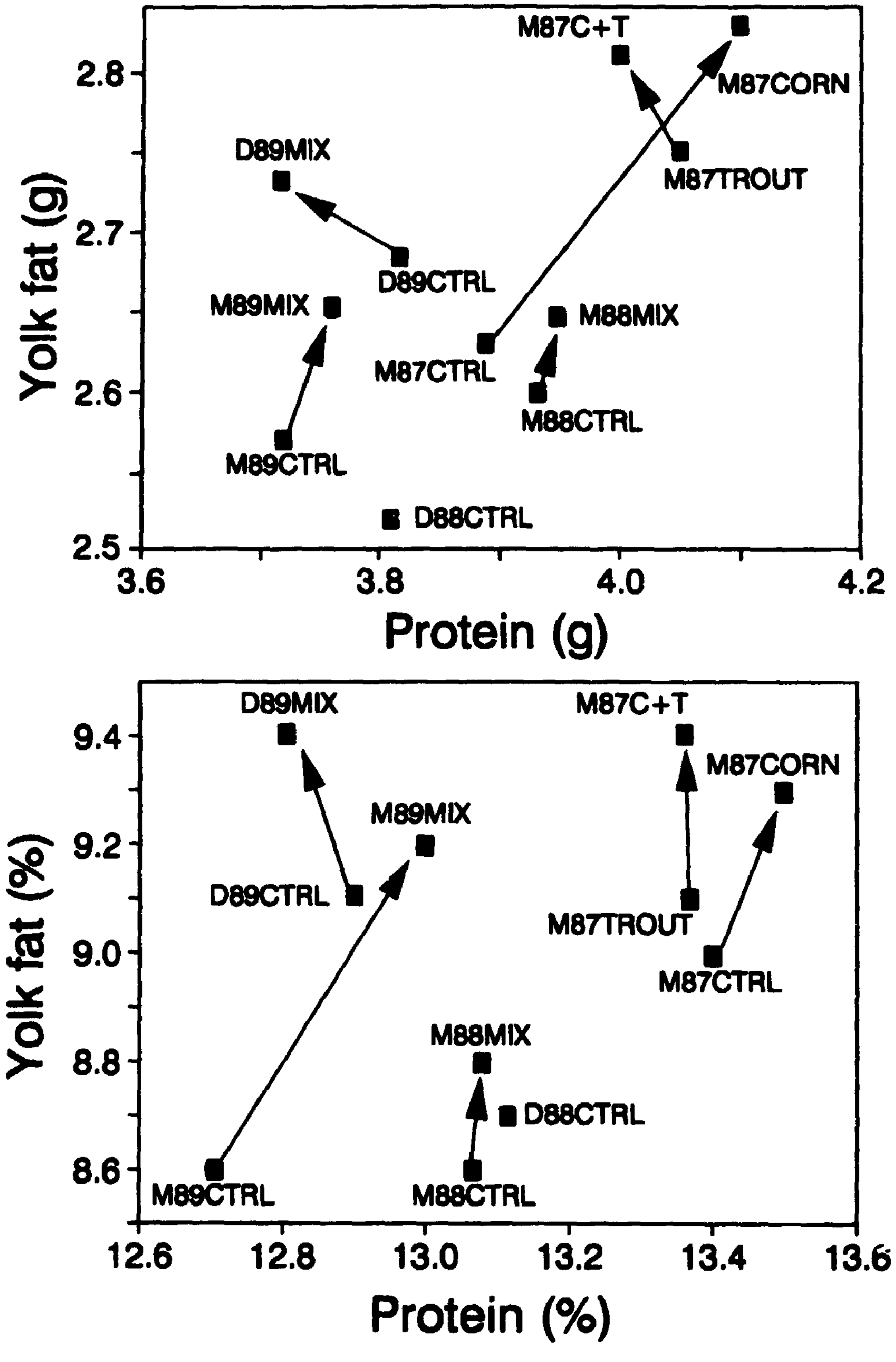


Fig. 4.3. Mean absolute (top) and proportional (bottom) fat and protein content of American Coot eggs in relation to year and supplemental food. Arrows connect sample groups with and without access to supplemental corn.

five feeding experiments that added corn to the diet of laying coots resulted in five increases (mostly nonsignificant) in absolute and proportional content of yolk-fat (sign tests, 1-tailed, P = 0.03). No such overall effect was apparent for protein content (Fig. 4.3; with trout chow being the relavent food supplement in 1987).

It is not clear why feeding effects would be most pronounced in 1987, when eggs were already of high nutritional quality. If egg quality is proximately affected by food availability, then supplemental feeding should have had major effects in 1988 and 1989, when overall egg quality was lower (Fig. 4.3). However, there were no effects in 1988, and the effects in 1989 were barely significant and did not bring egg quality in line with that of 1987 eggs (Table 4.3, 4.4; Fig. 4.3). This suggests that the different feeding protocol in 1987 may have influenced egg composition. The unbalanced nutritional quality of high-carbohydrate (corn) or high-protein (trout chow) diets may have flooded the birds' systems with excess nutrients of one particular kind, and these excess nutrients may have been dumped into eggs. Among domestic chickens, there is some general support for the "you are what you eat" hypothesis as it relates to nutrient content of eggs (Fisher 1969, Begin and Insko 1972, Butts and Cunningham 1972). This hypothesis can undoubtedly be better addressed in captive situations where investigators have complete experimental control over animal diets, but such experiments might have little relevance to wild birds on natural diets.

A few studies have examined the effect of diet quality on egg composition of wild birds breeding in captivity (e.g., Krapu and Swanson 1975, Krapu 1979, Beckerton and Middleton 1982, Eldridge and Krapu 1988). Although these studies have demonstrated that egg composition may vary in response to diet, the experimental diets were often extremely deficient (e.g., wheat only in the "Krapu" studies).

Only one other investigator has published information on the effect of supplemental food on egg composition among wild free-ranging birds. Hochachka (1988) found no differences in egg protein or lipid content between supplemented and unsupplemented Black-billed Magpies (*Pica pica*). The only significant difference he found was that relatively large eggs from control birds contained relatively less water (Hochachka 1988). However, this "effect" appears to have been heavily influenced by a single outlying data point from a control clutch (Hochachka 1988: Fig. 1), although similar results were apparently obtained in another study of Black-billed Magpies (Clarkson 1984 [Ph.D. thesis], *in* Hochachka 1988).

4.4.3 *Annual variation in egg composition.*

There was pronounced annual variation in both absolute and proportional egg composition. For absolute composition, only yolk-lean was individually affected. The most pronounced effect was on the pattern of covariation of yolk-lean with yolk-fat, with the relationship being much weaker in 1988. Generally, researchers have focused on lipid content of the yolk when evaluating egg quality (e.g., Ankney 1980, Alisauskas 1986). Duncan (1988), however, experimentally removed yolk sacs (i.e., deutectomy) from hatchling Northern Pintails (*Anas acuta*) and measured their ability to grow and to survive temporary periods of starvation. He concluded that the importance of lipid to newly-hatched chicks has been overemphasized, and that the nonlipid portion of the yolk may constitute a more critical reserve for hatchlings. If Duncan's results are generally true among birds, then the effects of supplemental food on lean yolk content of coot eggs, as observed in my study, might have important fitness implications.

After controlling for egg-size variation, there was significant annual variation in all components except relative shell mass and relative yolk-fat (variation in yolk-fat was suggestive, $P = 0.10$). I verified these annual patterns by analyzing fed groups only; the same general patterns emerged, although this interpretation is confounded by the different feeding methods used in 1987. These year effects were also apparent among coots nesting at Delta Marsh (Fig. 4.3), which is 110 km away from Minnedosa and in an entirely different wetland system, with more stable water-levels.

I can posit three explanations for this annual variation: (1) It reflects annual variation in feeding conditions on either the wintering grounds or on the spring migration corridors, which in turn affects annual variation in levels of nutrient reserves carried to the breeding grounds (e.g., Heitmeyer and Fredrickson 1981, Alisauskas and Ankney 1985, Alisauskas 1988, LaGrange and Dinsmore 1988). (2) It reflects annual variation in age composition of the population, due to annual variation in local and/or continental patterns of recruitment (such annual variation is well known for waterfowl recruitment [e.g., Reynolds 1987], and age is known to influence many aspects of parental performance [Sæther 1990]). (3) Finally, and least interestingly, this variation might reflect annual variation in processing techniques; i.e., biases in laboratory procedures. The first two hypotheses can be evaluated with respect to among-individual variation in nutrient reserves, age, and egg composition. These analyses are reported in the next chapter (Section 5.3.6). The age hypothesis is not consistent with annual variation in local or continental coot production during the years of my study, which would suggest high numbers of yearling breeders in 1987, and an increasing age-structure through 1988 and 1989 (Didiuk and Caswell 1989). All eggs were analyzed in the same way, by the same competent technician (J. Amery), and it therefore seems unlikely that variation in processing techniques could be the cause of annual variation in the data. Sources and magnitudes of measurement error for egg composition are unknown for this study, but Rohwer (1986*b*) found negligible absolute errors in replicated proximate analyses of Blue-winged Teal eggs (0.9% for albumen protein, 3.0% for yolk protein, and 1.6% for yolk lipid). It is unknown what potential biases, if any, are present in such egg processing techniques as boiling, freezing (but see Ricklefs 1982), oven-drying, and ether extraction, although some of these techniques have been critically evaluated for carcass analyses and found to produce relatively consistent results (Kerr *et al.* 1982, Dobush *et al.* 1985).

I am aware of only two studies that have examined annual variation in egg composition. Birkhead and Nettleship (1984) detected annual variation in wet yolk mass of Common Murre (*Uria aalge*) eggs, and Meathrel *et al.* (1987) found annual differences in several components of Herring Gull (*Larus argentatus*) eggs (these mostly involved wet masses, but also included dry albumen). Given that significant among sample group variation in water loss was observed during egg processing in my study (see also Nisbet 1978, Ricklefs 1982), these annual differences in wet component masses should be regarded skeptically.

4.4.4 *Effects of laying sequence on egg composition.*

Alisauskas (1986: Table 4) showed that egg size and yolk lipid declined with laying sequence, though albumen and yolk-lean did not. Because Alisauskas did not include egg size as a covariate in these analyses, it is impossible to tell precisely what was happening to proportional egg composition, but it was clear that late-sequence eggs contained less fat than did earlier-sequence eggs.

I did not document either an absolute or a proportional decline in yolk-fat with laying sequence in this study. Proportional albumen content increased with laying sequence, whereas yolk-lean declined, resulting in no net change of protein content with laying sequence. These results do not invalidate those of Alisauskas (1986), since he collected multiple eggs from clutches in order to examine sequence effects, whereas I collected only one egg per clutch and tried to standardize for sequence effects as much as possible by collecting fifth-laid eggs. Nevertheless, I did analyze a large sample of eggs from a wide range of sequence positions (range = 3 to 11) using powerful multivariate techniques, and found no differences in lipid content with laying sequence. This suggests that declining lipid content may be confined to the last-laid eggs of the clutch. Since egg size *per se* declines with laying sequence among terminal-sequence eggs (Alisauskas and Ankney 1985, Arnold 1991), this does not necessarily indicate that late-sequence eggs are of proportionately poorer nutrient content. Arnold (1991) reviewed a number of potential hypotheses to explain trends in egg size with laying sequence (coots also exhibit an initial increase in egg size with laying sequence for about the first 3 to 6 eggs in the clutch), and concluded that these patterns may reflect physiological oddities of egg formation.

4.4.5 *Effects of clutch size and laying date on egg composition.*

Results based on egg composition strengthened arguments in Chapter 3 suggesting positive among-individual correlations with respect to egg quality, clutch size, and laying date. Not only did earlier nesting birds tend to produce larger clutches consisting of larger eggs, but those eggs, in almost all cases, contained proportionately more nutrients and proportionately less water than did eggs from late-nesting coots with small clutches of small eggs. These results provide further refutation of the hypothesis that egg size and clutch size should exhibit negative trade-offs (e.g., Lack 1967, Rohwer 1988, Lessells *et al.* 1989).

Only one analysis suggested a possible trade-off among timing of breeding, egg number, and egg quality. There were significant negative interaction effects of clutch size and egg size on dry mass, yolk fat, and total energy (the overall multivariate test was not quite significant, P = 0.07). The main effects of clutch size and egg size were positive and large, thus big eggs were of higher average quality, eggs from large clutches were of higher average quality, and even large eggs from big clutches were of higher average quality, but, eggs in the last category were not as high in quality as might be predicted based only on clutch or egg size information. This may constitute an allocational trade-off in the life-history tactics of American Coots, but if so, it is clearly unimportant to the general population.

Two studies of egg composition in waterfowl have revealed conflicting patterns with respect to covariation in egg composition, clutch size, and laying date. In Blue-winged Teal (*Anas discors*), egg composition did not vary with clutch size, or between initial and renest clutches, but egg quality (yolk-lipid) declined with laying date (Rohwer 1986*b*). In semi-captive Barnacle Geese (*Branta leucopsis*) the opposite was true: yolk components declined with clutch size, and between initial and renest clutches, but did not vary with laying date (Owen and West 1988).

4.4.6 *Among-wetland variation in egg composition.*

My analyses of among-wetland variation in absolute and proportional egg composition gave no support to the hypothesis that territory quality can influence egg quality among coots (Alisauskas 1986, Hill 1988).

I am unaware of any other studies that have examined variation in egg composition on a small habitat scale. Birkhead and Nettleship (1984) ascribed regional differences in wet yolk mass of Atlantic Puffin (*Fratercula arctica*) eggs to among-colony variation in food abundance, and Nisbet (1978) found similar differences in egg composition between two colonies of Common Terns (*Sterna hirundo*). Although American Coots exhibit pronounced differences in clutch size and laying date between the Minnedosa Study Area and Delta Marsh, Manitoba (Alisauskas and Ankney 1985; Arnold and Alisauskas *unpubl. data*), analyses of egg composition have not revealed any consistent differences in egg quality between the two areas (Fig. 4.3; Arnold, Alisauskas, and Ankney *in revision*).

4.5 SUMMARY

Although my analyses detected many significant differences in egg composition among and within different samples of coots, results were often inconsistent across years or supplemental feeding regimes, and were therefore difficult to interpret. Differences were generally modest; the "highest quality" eggs (M87CORN) contained only 10-12% more lipid, protein, and energy, on average, than did the "lowest quality" eggs (M89CTRL). Among studies which have documented potential survival advantages in relation to egg size, "big eggs" have averaged 15 to 60% larger than "small eggs" (Schifferli 1973, Nisbet 1978, Lundberg and Väisänen 1979, Ankney 1980, Rhymer 1988*a*; differences based on fresh egg mass, egg volume, or hatchling mass). It remains to be seen whether differences in egg composition of the magnitude documented in this study can affect survival of hatchling coots. One major difficulty in conducting such analyses, obviously, is that the potential fitness value of eggs that have been boiled, frozen, dried, and extracted is always going to be nil. However, the high within-clutch repeatability of egg composition observed in many species of birds may provide an avenue for successfully approaching this topic (e.g., Ricklefs 1984*a*).

CHAPTER 5. NUTRIENT RESERVE DYNAMICS OF BREEDING AMERICAN COOTS

5.1 INTRODUCTION

Lack (1967) hypothesized that clutch size among waterfowl was limited by the availability of food for egg-laying females. In support of this hypothesis (the "egg formation hypothesis"), Lack demonstrated that there was an inverse correlation between clutch size and egg size among waterfowl species; i.e., species producing relatively large clutches, on average, produced relatively small eggs. Lack's analysis and interpretation have since been discredited by Rohwer (1988), and additional studies have failed to find trade-offs between clutch and egg size within single species of waterfowl (Rohwer 1988, Rohwer and Eisenhauer 1989, Lessells *et al.* 1989). This hypothesized allocational trade-off was not present in coots either; in fact, individuals laying relatively large clutches tended to produce larger, more nutrient-rich eggs (Chapters 3 & 4).

However, Lack's original hypothesis was flawed. If exogenous food resources are abundant enough for waterfowl to produce an egg a day from daily foraging intake, then females should be able to continue laying daily eggs until food availability deteriorates markedly (Rohwer 1986*a*). However, the breeding seasons of most temperate waterfowl are long and asynchronous, and renesting is common (Sowls 1955, Keith 1961, Lokemoen *et al.* 1990), as in coots (see Chapter 3), implying that food supplies are sufficient for egg formation for well over a month. By this reasoning, females should be able to lay 40 or more eggs per clutch, which clearly doesn't happen (clutch size averages about 10 in coots and most temperate ducks; Table 2.1, Rohwer 1988: Appendix).

Ryder (1970) modified Lack's hypothesis by suggesting that clutch size was limited by the quantity of stored nutrients that females could devote to egg formation, not by the quantity of food available during egg-laying. Ryder developed this hypothesis based on his studies of arctic-nesting Ross' Geese, which begin nesting before food is generally available, and hence, must rely on stored nutrient reserves for clutch formation and incubation. Stronger support for the nutrient limitation hypothesis was provided by Ankney and MacInnes (1978), who showed that for arctic-nesting Lesser Snow Geese, potential clutch size was positively correlated with nutrient reserve levels among arriving females. No such correlation was apparent among females that had completed laying, and these birds had fed little or none during egg formation; i.e., nutrient reserves seemed to determine clutch size (Ankney and MacInnes 1978). Similar extensive reliance on nutrient reserves during egg formation has been demonstrated for other arctic-nesting geese and for colonial-nesting Common Eiders (Korschgen 1977, Raveling 1979, Ankney 1984, Parker and Holm 1990), but these studies have not established a correlation between nutrient reserve levels and potential clutch size.

Subsequent studies of temperate-nesting waterfowl have demonstrated that most species utilize nutrient reserves (especially lipid) during clutch formation (reviewed by Ankney and Alisauskas *in press*). White-winged Scoters and renesting Blue-winged Teal are the only known exceptions to this rule (Dobush 1986, Rohwer 1986*a*). However, most temperate-nesting waterfowl feed extensively during clutch formation (Drobney and Fredrickson 1979, Swanson *et al.* 1979), so clutch size cannot be absolutely constrained by levels of nutrient reserves, as in arctic-nesting geese. Thus, if nutrient reserves limit clutch size among temperate-nesting waterfowl, then these reserves must constitute essential supplemental nutrients for egg-laying females; i.e., females cannot produce eggs using only exogenous nutrients (Rohwer 1986*a*). One criticism of this argument is that females could simply alter their laying rates. By producing eggs at a slower rate (i.e., 1 egg every second day) they could meet all their nutrient demands exogenously by devoting more foraging time to the formation of each egg (Astheimer 1985, Ankney and Afton 1988). However, except for the Mergini, most temperate waterfowl produce an egg each day (Bellrose 1976), the typical avian rate (Lack 1968). Thus, an unstated assumption of the egg formation hypothesis is that laying rates are inflexible, even though females could seemingly increase their clutch size (and hence their reproductive success?) by reducing their rate of egg laying. The egg viability and nest predation hypotheses (Arnold *et al.* 1987) may provide a solution to this dilemma, but proponents of the egg formation hypothesis would have to concede that, in addition to nutrients, clutch size in temperate waterfowl is limited by temporal constraints affecting optimal length of the egg laying period. Conversely, proponents of the egg viability and nest predation hypothesis would have to concede that waterfowl are rate-limited in their ability to form eggs, otherwise laying rates of > 1 egg per day should have evolved (e.g., Arheimer 1978).

Many researchers have implied that nutrient reserves might also limit clutch size among birds with parentally-fed offspring (e.g., Jones and Ward 1976, Fogden and Fogden 1979, Pinowska 1979, Houston *et al.* 1983, Alisauskas and Ankney 1985, Hails and Turner 1985; but see Ankney and Scott 1980; Murphy 1986*a*; Krementz and Ankney 1986, 1988; Young 1989). Although many of these studies have shown that birds use reserves during egg formation, they have not conclusively demonstrated that reserves limit clutch size. Oftentimes the egg formation hypothesis has been invoked for birds other than waterfowl only because other hypotheses failed to explain clutch size, not because the egg formation hypothesis itself was critically tested (e.g., Lack 1964, Winkler 1985, Nur 1986; see Chapter 1).

For many birds, incubation may represent a more energetically stressful period than egg-laying (Ankney and MacInnes 1978, Jones 1987, Ankney and Afton 1988; but see Walsberg and King 1978). Thermal requirements of developing embryos demand that parents maintain high incubation constancy (Webb 1987), which often leaves incubating birds with little or no time available to forage (e.g., Ankney and MacInnes 1978, Afton 1979). Many species draw heavily on stored nutrient reserves during incubation; such a pattern is especially pronounced among large-bodied birds with uniparental incubation (e.g., penguins, waterfowl, and galliforms; reviewed in Moreno 1989*d*). Because failure to successfully complete incubation results in total reproductive failure (and sometimes, in death of the parent; Korschgen 1977, Ankney and MacInnes 1978), whereas failure to lay one or two additional eggs results in only partial reproductive loss, females that rely on nutrient reserves during incubation might be expected to err on the conservative side during laying (i.e., produce somewhat smaller clutches than would be energetically possible) in order to insure adequate reserves for incubation (Ankney and MacInnes 1978, Ankney and Alisauskas *unpubl. MS*).

Small-bodied birds have little capacity to store nutrients, and species with biparental incubation usually have adequate time to forage; both of these factor reduce the reliance of incubating birds on stored reserves (Moreno 1989*d*). However, many birds that maintain body mass during incubation undergo substantial weight loss during brood-rearing (Moreno 1989*d*). Generally, this applies only to those species that provide food to their dependent nestlings (i.e., altricial birds, Moreno 1989*d*), but male Lesser Snow Geese may utilize fat reserves while tending newly-hatched self-feeding goslings (Ankney 1977). Two alternative hypotheses have been advanced to explain weight loss among birds during incubation and brood rearing: 1) The breeding stress hypothesis suggests that this weight loss reflects a cost of reproduction; birds allocate energy into their eggs or nestlings at the expense of their own body maintenance (Yom-Tov and Hilborn 1981). 2) The optimal allocation hypothesis (my term) suggests that this mass loss is adaptive in that it reduces maintenance demands for the adult (and, in some species, allows for more efficient flight), thereby allowing more time and energy to be channeled into offspring (Freed 1981, Norberg 1981, Moreno 1989*d*).

Previous research has suggested that clutch size in American Coots may be constrained by the ability of females to form eggs (Alisauskas and Ankney 1985). Alisauskas and Ankney (1985) estimated that laying coots obtained 85% of their lipid and 28% of their protein from nutrient reserves. Of 10 temperate nesting waterfowl for which similar estimates are available (Dobush 1986, Ankney and Alisauskas *in press*), only Mallards and Canvasbacks obtained a greater proportion of their lipid requirments from reserves, and only American Wigeons obtained more of their protein this way. These findings suggest that the reproductive strategies of coots might be more similar to those of species with precocial self-feeding young (e.g., waterfowl) than to species with altricical or semi-precocial parentally-fed young (e.g., passerines, larids). Unlike most waterfowl (Afton and Paulus *in press*), coots did not use nutrient reserves during incubation (Alisauskas and Ankney 1985), as might be expected (e.g., Moreno 1989*d*) given their system of biparental incubation (Crawford 1977). Nutrient reserve dynamics of brood-rearing coots have not been examined previously, but based on Lack's brood-rearing hypothesis, adult coots should exhibit signs of negative energy budgets during the brood-rearing period.

In this chapter, I reassessed the relative importance of nutrient reserves to breeding American Coots. I began by examining variation in nutrient reserve levels across stages of the breeding cycle. Then I tested for changes in nutrient reserves (either use or storage) within specific stages of the annual cycle; these stages included prebreeding, egg formation, incubation, and brood-rearing. I also compared nutrient reserve dynamics of coots receiving supplemental food with those of coots obtaining natural foods only. Finally, I compared nutrient reserve levels of females collected during laying and incubation with characteristics of their clutch (i.e., date of laying, clutch size, egg size, and egg composition).

5.2 METHODS

I collected adult male and female coots throughout the breeding season. Many of these birds had known nesting histories; they were shot as they flushed from their nests in the early morning (05:00 to 07:00) or were trapped on their nests at night (Crawford 1977). A few coots were nest-trapped, aged, weighed, measured, and then released; data from these birds were used in analyses comparing clutch size and laying date with attributes of the laying female. Other coots were collected before they began nesting, or were shot in open water; these birds could not be assigned with certainty to any particular nest. Reproductive status of these birds was inferred from ovarian characteristics, presence/absence of a brood patch, stage of molt, and/or nesting chronology of the population at large (see beyond).

5.2.1 *Carcass dissections.*

On the day of collection, coots were weighed (± 1 g, triple-beam balance) and 14 external morphological measurements were taken: total length, wing length, wing chord, tarsus length, middle toe length, middle claw length, hind toe length, culmen length, bill length, bill height, bill width, culmen width, head length, and head width (± 1 mm as measured with a flat ruler for total length, wing length, and wing chord; all other measurements ± 0.05 mm as measured with dial calipers) (all measurements as defined by Alisauskas 1987, except bill length and culmen width as defined by Petrie 1988). After assessing measurement error of these variables, I elected to exclude wing length, hind toe length, bill width, and head width from future analysis (Appendix 3). Age classes (1, 2, 3, or ≥ 4) were assigned by examining the color of the tarsus and tibiotarsus, as described by Crawford (1978). Crawford's technique is fairly subjective, so I also included intermediate subdivisions between his major age classes (i.e., 1/3, 1/2, and 2/3). I found fairly high measurement error using Crawford's aging technique (Appendix 3). Moreover, Visser (1986) has critically examined this technique for European Coots and has concluded that tarsal coloration is correlated with age, but only crudely. Age classes (yearling/adult) were therefore independently assessed based on presence/absence of the bursa of Fabricius, but as far as I am aware, this technique has not been critically evaluated for coots. Consequently, I have interpreted tarsal coloration and bursa characters only as approximate indicators of age.

Coots were plucked to remove all flight and contour feathers; plucking was conducted either on the day of collection or after the carcasses had been frozen and subsequently thawed.

Female coots were opened on the day of collection and the ovary and oviduct were removed and stored in 10% formalin. The remaining carcass was sealed in double plastic bags and frozen until subsequent laboratory analysis. Thawed carcasses were weighed (± 0.1 g) and dissected to remove the esophagus, gizzard, small intestine, large intestine, bursa of Fabricius, ceca, liver, pancreas, spleen, and heart. Lengths of ceca (both combined), small intestine, large intestine, and bursa of Fabricius were measured to the nearest 1 mm. All organs were cleaned of adhering fat and weighed wet (± 0.01 g); digestive organs were reweighed after removing their contents. Ingesta mass was determined as the sum of all digestive organ contents. Visible fat deposits were removed from the visceral cavity and added to any that had been removed from individual organs; this fat (referred to as abdominal fat) was weighed and discarded. For male coots, the testes were weighed wet and discarded. The left breast and leg muscles (as defined in Ankney and MacInnes 1978) were dissected free and weighed wet. The feet were removed from the carcass (just above the tarsometatarsus-tibiotarsus joint) and were excluded from the following analyses. All organs, except the liver and breast and leg muscles, were combined with the remainder of the carcass and ground twice in a Hobart meat grinder. This homogenate, or an approximately 300-g subsample of this homogenate for large birds, was dried to constant weight at 90°C (Kerr *et al.* 1982). The liver, left leg muscle, and left breast muscle were dried seperately. Dried samples were weighed (± 0.01 g) and homogenized to a fine powder using an electric coffee grinder.

Lipid content of dried liver, leg, breast, and carcass homogenates were determined by petroleum ether extraction in a modified Soxhlet apparatus (Dobush *et al.* 1985). Lean dry weights (LDW) of the liver, leg, and breast muscles were assumed to consist entirely of protein (e.g., Ankney and Afton 1988). Lean dry samples of carcass homogenates were ashed in a muffle furnace at 550°C for 6 hr. All oxidized material was assumed to be protein, and remaining residue was used to calculate total ash content of the carcass. Estimated protein fractions of the carcass, leg, breast, and liver homogenates were summed to obtain total protein reserve, and the lipid content of these homogenates were summed with abdominal fat to obtain the total fat reserve.

5.2.2 *Ovarian analysis.*

The preserved ovaries of collected females were examined to determine numbers of developing, postovulatory, and atretic follicles (Payne 1965, Scott and

Ankney 1983). All developing or atretic follicles ≥ 7.5 mm in diameter were removed, weighed wet (± 0.01 g), individually dried at 80°C, and reweighed. Wet and dry weights were also obtained for the remainder of the ovary and the oviduct. Lipid and protein content were determined for 45 individual follicles using petroleum ether extraction; I used these data to construct estimates of daily follicle growth. Coots usually laid one egg per day (Section 3.3.6), implying a daily size progression among developing follicles, although this may not have been true during early follicle growth (e.g., Barzen and Serie 1990). For remaining ovaries, the individual follicles were combined and lipid content was determined in sum. Follicles of some birds were damaged and could not be identified with certainty. By assuming that coots with damaged follicles had the same average follicular development hierarchy as did coots with undamaged ovaries, I could estimate the original size and the amount of lost nutrients from damaged follicles. Such ambiguities had little effect on estimates of nutrient commitment to reproduction because most developing follicles contain very few nutrients. However, I had to exclude such birds from some analyses because it was unclear how many additional eggs they were likely to lay.

The number of eggs laid by collected birds was determined from nest information, or for birds of unknown nesting history, by number of postovulatory follicles (POF's). These two estimates should coincide, but they frequently did not (Fig. 5.1). Although there are several factors that could bias the nest information (i.e., intraspecific parasitism, partial clutch depredation, renesting; Kennedy *et al.* 1989), I was able to correct for most of this bias (i.e., I knew 4 nests had been parasitized and I excluded the parasitic eggs; I knew that there were no previously destroyed nests on these wetlands, so renests were very unlikely). Moreover, the rates of parasitism and renesting necessary to produce the lack of fit in Figure 5.1 greatly exceed estimates of parasitism and renesting frequencies based on nest visits (Arnold, *unpubl. data*). I suspect that my inability to correctly identify regressed POF's was the most prominent source of bias (Scott and Ankney 1983, Krementz and Ankney 1988). Low counts of POF's were especially pronounced among known postlayers (Fig. 5.1), implying rapid

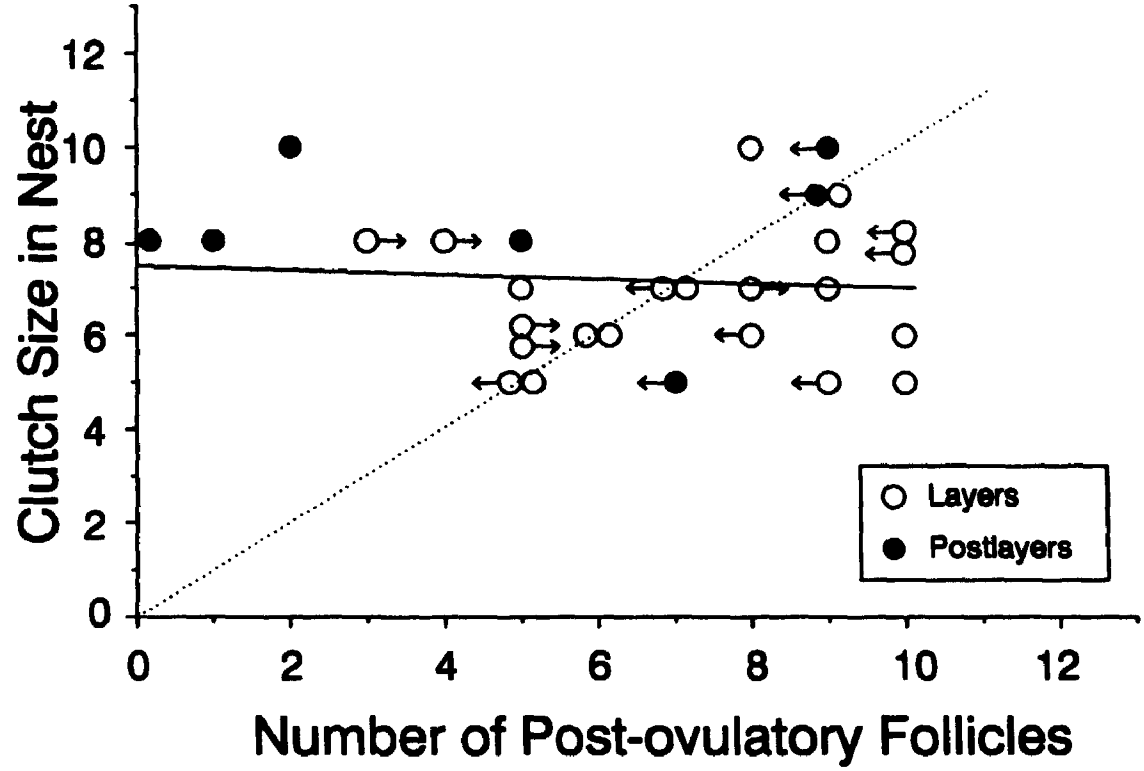


Fig. 5.1. Number of eggs in nests of collected female coots in relation to visual assessment of the number of post-ovulatory follicles (POF). Counts of POF were made without knowledge of clutch size (CS). Postlayers were collected 1 - 4 d postlaying. CS of four nests known to have been parasitized by conspecifics were corrected before plotting data (all four changes resulted in improved fit). Arrows indicate recorded uncertainty about actual number of POF; e.g., the postlayer with POF = 9, CS = 10 in the upper right corner was recorded on the lab data sheet as: 9 (7-9 ?). Nine of 14 recorded uncertainties lead to better fit (e.g., towards the dashed line with b = 1). Actual relationship is indicated by solid line (P > 0.8).

follicular resorption after clutch completion.

Despite the poor correlation between number of POF and actual clutch size, I nevertheless included these females in my analyses for the following reasons. Although estimates of POF's were not correlated with number of eggs known to have been laid, the range of variation in POF (3 - 10) and clutch size (5 - 10) for laying females both centered around 6 - 8 eggs laid. It was clear that birds with POF had laid some eggs, and birds without POF and brood patches had not. Even this crude level of distinction in measuring reproductive investment should have been sufficient to produce a relationship between nutrient reserves and investment in clutch formation, *if* such a relationship existed. However, if such a relationship existed, then use of this data could lead to a biased, or at least murky, estimate of the true relationship. Almost all birds for which "true" clutch size (based on nest information) was unknown were collected in 1987. Thus any consistent bias introduced by using data based on POF should have been manifested as a significant year effect. In subsequent figures, the 1987 data are clearly indicated. Finally, analyses conducted using only the sample of known-nest birds did not qualitatively alter any of my conclusions.

Female coots were categorized into reproductive stages according to the following attributes. *Arrival* included female coots with no vascularized and yolky ovarian follicles > 5 mm in diameter. Arrival coots were collected prior to the first known nest initiation of the year. This category combines the arrival and paired categories of Alisauskas and Ankney (1985). Most of the arrival birds I collected were not associated with flocks, and therefore were probably paired, but I could not always verify pairing status. *Laying* included coots that were either prelayers (i.e., rapid follicle growth [RFG], at least one vascularized and yolky follicle ≥ 5 mm, but no postovulatory follicles) or layers (at least one postovulatory follicle and at least one large developing follicle ≥ 15 mm, and/or an oviducal egg). Postlayers had postovulatory follicles, but no large (≥ 15 mm) non-atretic follicles (criteria modified from Alisauskas and Ankney 1985, Krementz and Ankney 1988, Barzen and Serie 1990). For coots collected from known nests, postlayers were limited to birds that had completed their clutch within the last 0 - 4 days. For coots with unknown nesting histories, postlayers were limited to birds with an oviduct dry mass of ≥ 0.75 g (of coots with known nesting histories, 9 of 11 [82%] collected 1 - 4 d postlaying had an oviduct dry mass ≥ 0.75 g, whereas only 1 of 8 [13%] collected > 4 d postlaying had an oviduct dry mass > 0.75 g; exceptions were collected on days 3, 4, and 6). Incubation included coots collected or nest-trapped from completed clutches with known initiation dates; females with brood patches that were identified as postlayers by ovarian examination were also included in this category. Postlaying and early incubation represent the same categories; birds were called one or the other depending on the analysis being performed (i.e., postlayers for analyses of egg-laying energetics, incubation for analyses of incubation energetics and for the overall cross-seasonal analysis). Early brood-rearing included male and female coots collected while tending dependent offspring ≤ 150 g. Because of asynchronous hatching, early brood-rearing and incubation categories exhibited some overlap; I assigned coots collected during this overlap period (n = 3 coots) to the activity they were involved in when collected (all three were incubating). Late brood-rearing included males and females that had not yet shed their primaries and were collected after all known nests had hatched. Because there was very little parental investment occurring at this stage (e.g., Ryan and Dinsmore 1979, Desrochers and Ankney 1986), not all coots in this category could be positively identified as breeders (parent-offspring cohesiveness was minimal, brood patches were replaced by new feather growth, and many coots moved to different wetlands in response to pond drying). Some late nesting coots overlapped wing molt with brood rearing (C. D. Ankney and T. W. Arnold, *unpubl. data*); these coots were identified as late brood-rearing only if they were collected with an attendant chick. Some males could not be unambiguously assigned to reproductive categories; I assigned reproductive categories to these birds based on available morphological information (i.e., presence/absence of brood patch, testes size, molt intensity) and by comparing date of collection with breeding chronology of the population at large (e.g., Krementz and Ankney 1988).

Reproductive nutrients of prelaying, laying, and postlaying females were calculated as the sum of all fat, protein, or ash contained in ovarian tissues (ovary, follicles, oviduct, oviducal egg) and previously laid eggs (e.g., Ankney and Afton 1988). Nutrient content of previously laid eggs was estimated by the product of number of eggs laid times mean nutrient content per egg. Number of eggs laid was based on nest information if available, or post-ovulatory follicle information if not. Because post-ovulatory follicles of postlayers could not be assessed, even approximately (Fig. 5.1), I excluded postlayers of unknown nesting history (including all 1987 data) from analyses involving reproductive nutrients. Mean nutrient content per egg was estimated from one of the following methods (in descending hierarcy of preference): (1) an analyzed egg from the clutch (including oviducal eggs), (2) allometric relationships between nutrient content and egg volume (for clutches with measured but unanalyzed eggs; based on equations in Chapter 4, after adjusting for the relationship between volume and fresh mass), or (3) mean nutrient content per egg from the study population at large, which ignores individual variation in egg composition and may introduce errors of ± 15% in estimates of lipid content (e.g., Arnold, Alisauskas, and Ankney, *in revision*).

5.2.3 *Statistical analysis.*

Alisauskas and Ankney (1987) provided methods and rationale for statistically controlling body (structural) size variation in analyses of nutrient reserve dynamics. I employed such corrections in most analyses (Appendix 5), but I disagreed with the logic of such an approach for analyses of laying females, and therefore did not correct for body size in these analyses. Because nutrient reserves of laying females are presumably being used for egg production, it is the absolute quantity, not the size-adjusted quantity, that determines how many eggs can be laid (especially as regards lipid; protein and ash are more problematic). Individual females may have more fat available for egg production precisely because they are larger than other females (e.g., Alisauskas 1988, Alisauskas and Ankney 1990); however, such additional fat would disappear into the statistical netherworld if I employed body size adjustments.

Mean sizes of nutrient reserves were compared among reproductive categories using ANOVA; following significant ANOVA, temporally adjacent means were compared using least significant difference (LSD) tests. To more precisely determine nutrient reserve dynamics of laying females, I used a regression approach developed by Alisauskas and Ankney (1985):

$$\text{Nutrient reserve} = a + b(\text{reproductive nutrient}).$$

This equation ignores maintenance-energy costs of the laying female, but these costs are likely to be higher than egg-formation costs in many birds (A. D. Young, *pers. comm.*), including American Coots (Alisauskas and Ankney 1985). Because activity budgets are typically unknown, investigators have typically inferred that nutrient reserves are used for maintenance in addition to egg formation if $b \geq 1.0$ (Barzen and Serie 1990).

I used a similar regression approach to assess nutrient reserve dynamics during incubation:

$$\text{Nutrient reserve} = a + b(\text{day of incubation}).$$

Due to low sample sizes, I combined males and females for analysis. I tested for additional effects of sex, year, and supplemental food by including appropriate dummy variables in the preceding regression equation (i.e., ANCOVAs). I also evaluated potential effects of laying date and age class by including these continuous variables in the regression model.

5.3 RESULTS

Annual variation in nutrient reserves by sex and reproductive category was statistically significant overall (MANOVA: $F_{(10,378)} = 3.59$, $P = 0.0001$) and in 6 of 63 individual comparisons (9.5%). Differences in total fat were highly significant among females in the arrival category ($P < 0.003$); these differences were attributable to larger masses among the 1989 sample of birds. Because very few coots were collected in 1989 ($n = 11$, 10 of these in the arrival category), and because most of these birds were likely transients (few birds stayed on the study area to breed), I deleted 1989 birds from the following analyses. With 1989 data deleted, year effects were still slightly significant (MANOVA: $F_{(5,178)} = 2.60$, $P = 0.02$), but only 4 comparisons were individually significant (6.4%; all at $P = 0.01$ to 0.04). Based on these results, I elected to pool 1987 and 1988 data for subsequent analyses. Data were insufficient in most cases to justify separate analyses, and more importantly, 1987 data were incomplete, thus year effects could usually not be included in models involving interactions.

5.3.1 *Nutrient reserve dynamics of coots: general patterns throughout the breeding season.*

Female coots exhibited little variation in body composition with respect to breeding activity. Although body mass fluctuated significantly, levels of fat, protein, and ash remained similar from arrival through brood-rearing (Table 5.1). Ingesta mass varied significantly with breeding activity, with females containing low quantities of ingesta during laying and incubation, and high quantities during brood-rearing (Table 5.1).

Males exhibited significant variation in lipid and ingesta mass throughout the breeding cycle, and near-significant variation in body mass (Table 5.1). Significant changes occurred between early and late brood-rearing, when mean fat levels increased, and during incubation, when ingesta levels were lower than during either the laying or early brood-rearing periods (Table 5.1).

Male coots are structurally larger than females, so not surprisingly, they weighed more and contained absolutely larger nutrient reserves and ingesta quantities than did females (Table 5.1). However, males also contained proportionately larger lipid reserves (relative to lean dry mass) during all breeding stages except early brood-rearing (Table 5.1).

5.3.2 *Nutrient reserve dynamics of pre-breeding coots.*

After arriving on the breeding grounds, female coots did not accumulate nutrient reserves in preparation for breeding; in fact, protein reserves declined slightly with collection date ($b = -0.36$ g per d, $F_{(1,42)} = 4.39$, $P = 0.04$; protein reserves were corrected for variation in structural size). I suspect that this

Table 5.1. Body mass, nutrient reserves, and ingesta mass of unsupplemented male and female American Coots, 1987 & 1988.

Variable:	Arrival	Laying	Incubation	Early Brood-rearing	Late Brood-rearing	F	P
Females:	(44)[a]	(23)	(17)	(6)	(9)		
MASS	520.2 + 59.8	* 563.0 + 43.6	* 515.2 + 51.5	561.5 + 32.1	523.9 + 47.5	3.50	0.01
FAT	22.9 + 15.7	16.7 + 8.9	18.6 + 12.7	23.7 + 15.3	21.5 + 14.3	0.94	0.44
PROTEIN	81.7 + 10.2	81.2 + 8.5	83.0 + 5.8	81.0 + 5.9	77.3 + 8.9	0.63	0.64
ASH	13.5 + 1.9	14.2 + 2.6	14.1 + 1.3	14.4 + 1.2	13.7 + 2.3	0.71	0.59
INGESTA	24.8 + 10.2	* 16.4 + 7.1	14.6 + 8.0	* 49.4 + 11.0	* 31.5 + 11.4	20.36	0.0001
Males:	(39)	(21)	(12)	(6)	(20)		
MASS	674.8 + 69.3	670.7 + 66.0	628.3 + 63.5	687.4 + 28.2	698.1 + 67.3	2.19	0.08
FAT	33.9 + 20.3	26.3 + 14.5	33.1 + 16.4	24.2 + 14.8	* 45.3 + 24.3	2.90	0.03
PROTEIN	108.5 + 11.8	112.3 + 12.1	110.5 + 12.1	105.8 + 5.9	104.3 + 13.5	1.27	0.29
ASH	18.5 + 2.6	18.7 + 2.6	17.6 + 1.8	17.5 + 2.8	19.1 + 2.8	0.89	0.47
INGESTA	34.5 + 13.3	33.3 + 15.7	* 18.2 + 9.5	* 57.8 + 10.7	49.7 + 18.1	12.74	0.0001

Notes: Adjacent means separated by * are significantly different (LSD tests). All variables differed significantly between the sexes (males larger, $P < 0.0001$). There were no sex*stage interaction effects ($P \geq 0.09$).

[a] (Sample size).

seasonal decline was not due to changes occurring within individual females, but to changes occurring within the study population over the course of the collection period. Younger female coots (as indexed by tarsus color) arrive later on the breeding grounds (Alisauskas and Ankney 1985), and have smaller protein reserves (Alisauskas and Ankney 1987). When I included age (tarsus color) in the above analysis it had a significant effect ($P = 0.02$), but the date effect became even more significant ($P = 0.01$).

Among arrival males, there was a significant decline in body mass with collection date ($b = -2.6$ g per d, $F_{(1,37)} = 4.62$, $P = 0.04$), and near significant declines in fat and protein reserves ($b = -0.63$, $P = 0.09$; $b = -0.39$, $P = 0.07$, respectively). Body and protein reserves were related to age, though fat reserve was not ($P = 0.08$, 0.02, 0.89, respectively), but date effects remained significant after controlling for age.

5.3.3 *Variation in nutrient reserves during egg-laying.*

Among unsupplemented coots, nutrient reserves did not vary with nutrient commitment to reproduction (Table 5.2: fat declined and protein and ash increased, all nonsignificantly). The overall regression slopes (which included food-supplemented birds) indicated nonsignificant increases in both fat and protein reserves with increasing reproductive investment (Fig. 5.2). Other factors did affect the size of nutrient reserves: fat reserves declined with collection date and increased with age; protein reserves varied annually (higher in 1987) and seasonally (declined with date); and mineral reserves varied with age (lower in yearlings than in adults) (Table 5.2). Supplementally-fed females had greater fat and protein reserves than did unfed females, but mineral reserves were unaffected by supplemental feeding (Table 5.2, see also Fig. 5.2). There were no significant interactions among these variables (Table 5.2).

The number of developing follicles in females approaching clutch completion ($\leq$ 4 developing follicles) was independent of carcass fat, protein, mineral, and ingesta (see Fig. 5.3 for fat and protein). The number of atretic follicles in females that had just completed their clutches was likewise

Table 5.2. Factors affecting nutrient reserves of laying[a] female American Coots.

Effect:	Fat	Protein[b]	Ash[b]
Reproductive nutrient (RN)[c]	0.65, 0.43, -0.13[d]	0.04, 0.84, 0.02	0.07, 0.79, 0.02
Year	0.66, 0.42, 3.30	7.12, 0.01, 7.34	1.47, 0.23, 1.07
Year * RN	3.01, 0.09, --	0.02, 0.90, --	0.19, 0.67, --
Date	13.56, 0.0007, -0.88	6.40, 0.02, -0.33	1.93, 0.17, -0.05
Date * RN	0.10, 0.76, --	0.23, 0.63, --	0.10, 0.75, --
Bursa	5.23, 0.03, -8.67	1.47, 0.23, -3.31	5.10, 0.03, -1.66
Bursa * RN	2.78, 0.10, --	0.01, 0.92, --	0.55, 0.46, --
Food	6.46, 0.02, 12.00	4.50, 0.04, 5.90	0.02, 0.89, -0.11
Food * RN	1.80, 0.19, --	1.23, 0.28, --	2.77, 0.11, --

Notes: Main effects were analyzed singly; interactions were analyzed in conjunction with main effects. Supplementally-fed birds were excluded from all analyses except for Food and Food * RN. 1987 data and all prelayers were excluded from analyses involving Food (no fed birds were collected in 1987, and only one late-season fed prelayer was collected). All effects remained significant when tested against other single variables, except for Food effect on Fat Reserve, which declined to P = 0.06 when Date was included in the model.

[a] "Laying females" includes females in rapid-follicle development, actual layers, and postlayers within 4 d of clutch completion.

[b] Protein and Ash reserves, but not Fat, were corrected for variation in structural size (see text).

[c] Reproductive Fat for analyses of Fat Reserve, Reproductive Protein for Protein Reserve, Reproductive Ash for Ash Reserve.

[d] Data are F, P, and b from ANOVA or ANCOVA. Regression coefficients are provided for main effects only; for Year, positive coefficients indicate larger reserves in 1987; for Bursa, negative coefficients indicate smaller reserves among yearling birds; for Food, positive coefficients indicate larger reserves among food-supplemented birds.

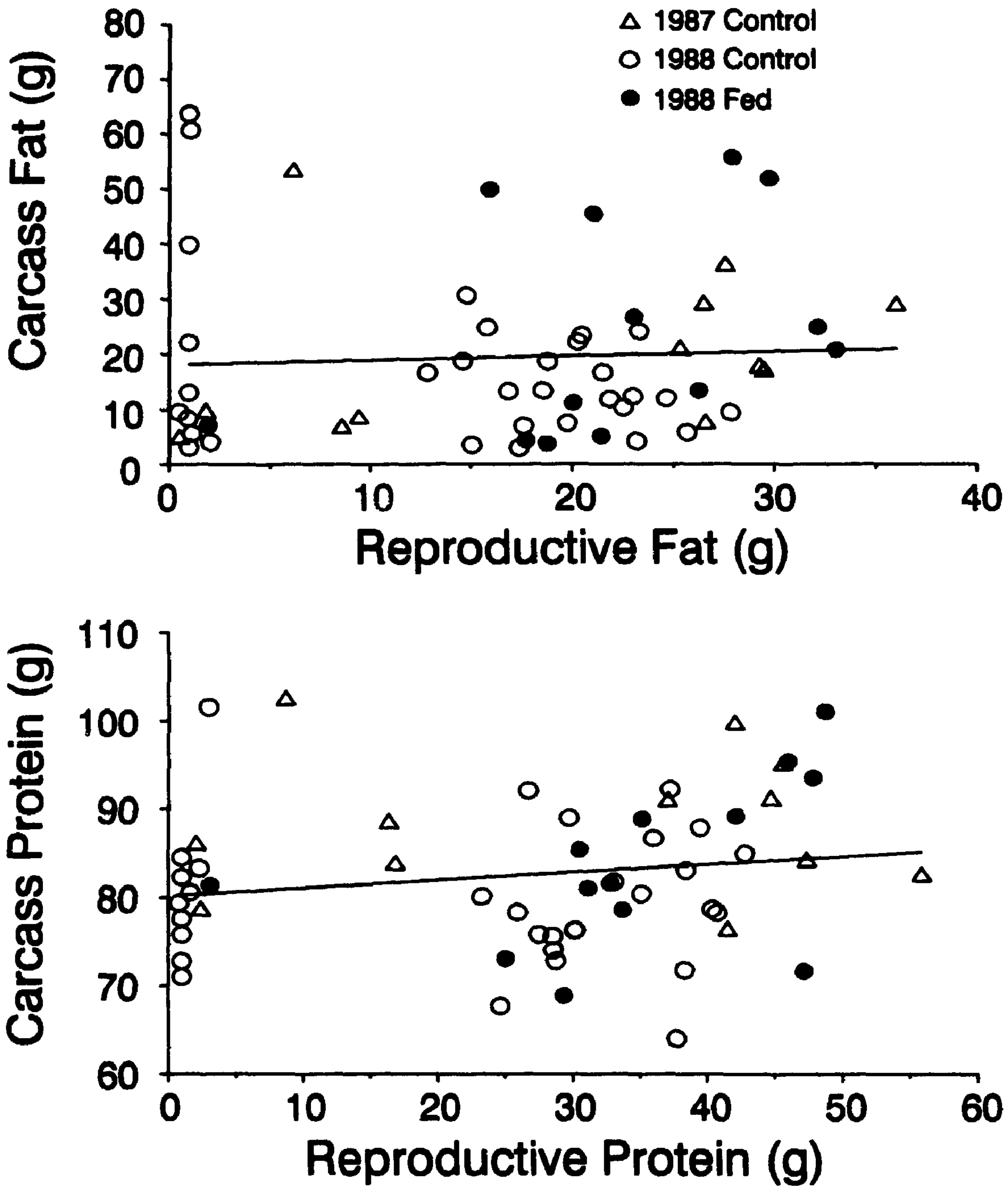


Fig. 5.2. Nutrient reserve dynamics of laying female American Coots (n = 57). Trend lines are fitted to all data (1987, 1988-Ctrl, and 1988-Fed); these relationships were not statistically significant. Data points along lower left axis in each plot were shifted horizontally for easier viewing; these birds had < 1 g of reproductive fat and reproductive protein. Triangles denote 1987 birds, for which reproductive nutrients were estimated from post-ovulatory follicle data (see text).

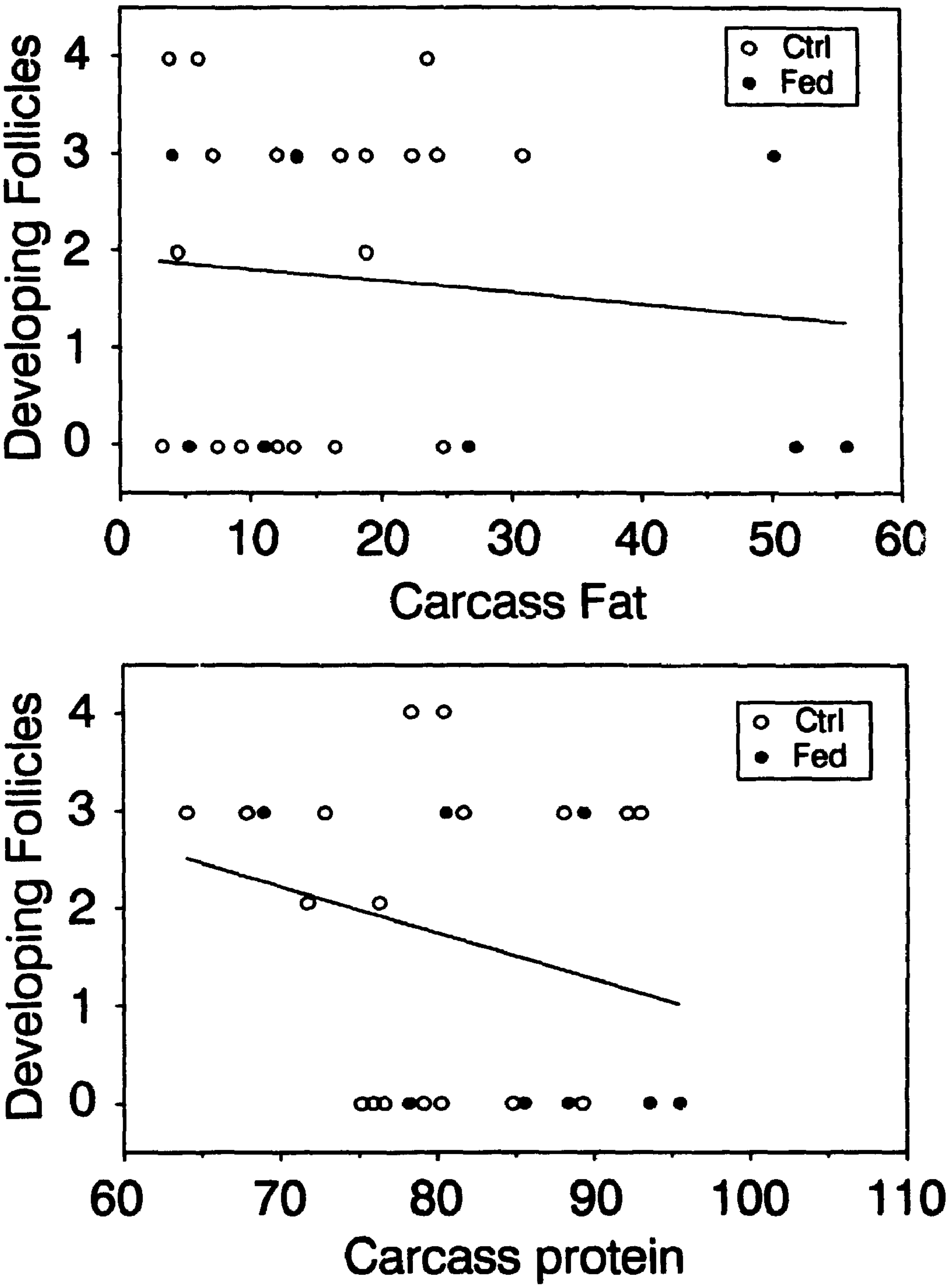


Fig. 5.3. Numbers of developing follicles among late-laying female American Coots in relation to size of their nutrient reserves. Trend lines were fitted to all data; they were not significant.

independent of nutritional status ($r^2 \leq 0.01$, $P \geq 0.73$, $n = 13$).

Male coots also maintained their nutrient reserves during the laying period (Table 5.1), but supplementally-fed males exhibited a much larger increase in body fat (relative to unsupplemented males), than did supplementally-fed females (relative to unsupplemented females) (Table 5.3).

5.3.4 *Nutrient reserve dynamics of incubating coots.*

Fat reserves increased, on average, by 1.3 g per day throughout incubation (Fig. 5.4). Rate of fat increase did not differ between the sexes, or between supplementally-fed and control coots; however, male coots averaged approximately 1.6 times more fat than females, and fed coots averaged approximately twice as much fat as unfed controls (Table 5.3). There were no significant interactions among these variables ($P \geq 0.40$).

Protein reserves (corrected for structural size variation across both sexes) did not change during incubation, nor were protein reserves influenced by supplemental food (Fig. 5.4). However, when analyses were conducted separately for each sex (including a different body-size adjustment based on within-sex variation), fed females had significantly larger protein reserves (Table 5.3). A similar, nonsignificant trend was evident among males (Table 5.3).

5.3.5 *Use of nutrient reserves during the brood-rearing period.*

There were no changes in body mass with collection date during brood-rearing, nor was body mass affected by supplemental feeding, but "old" coots weighed more than "young" coots (Table 5.4). Fat reserves increased during brood-rearing, and among coots receiving supplemental food (Tables 5.3 and 5.4). Effects of supplemental feeding on body fat were confounded with age effects, with younger birds apparently benefitting more from additional food (Table 5.4). Fat levels did not vary between sexes, in marked contrast to body mass, protein, and ingesta masses. Protein reserves declined with date, but only among younger birds. Fed birds averaged 6.5 g more protein than unfed birds (Table 5.4). Ingesta mass declined with collection date, and was lighter among birds receiving

Table 5.3. Body mass, nutrient reserves, and ingesta mass of American Coots in relation to supplemental feeding.

Variable:		Laying	Incubation	Late Brood-rearing
Females:		(17/7)	(11/9)	(9/4)
MASS	Ctrl	551.5 + 40.2	494.3 + 48.3	523.9 + 47.5
	Fed	578.6 + 53.8	526.0 + 42.3	554.9 + 17.4
FAT	Ctrl	15.5 + 8.0 *	18.6 + 15.1 *	21.5 + 14.3 **
	Fed	29.2 + 21.4 *	38.6 + 26.4 *	53.9 + 22.5 **
PROTEIN	Ctrl	78.9 + 8.1 [a]	81.1 + 4.9 *	77.3 + 8.9 *
	Fed	83.7 + 10.3 [a]	87.0 + 5.5 *	87.8 + 3.4 *
ASH	Ctrl	13.9 + 2.5	13.8 + 1.2	13.7 + 2.3
	Fed	14.3 + 1.9	13.3 + 2.3	14.5 + 1.0
INGESTA	Ctrl	16.9 + 7.8	15.0 + 9.7	31.5 + 11.4
	Fed	14.8 + 5.5	11.4 + 3.5	27.1 + 13.1
Males:		(9/5)	(10/8)	(20/10)
MASS	Ctrl	659.3 + 82.2	622.0 + 65.1	698.1 + 67.3
	Fed	695.5 + 91.3	663.4 + 71.8	652.2 + 26.0
FAT	Ctrl	23.1 + 10.2 **	33.3 + 16.4 [b]	45.3 + 24.3
	Fed	63.4 + 39.2 **	45.4 + 33.8 [b]	55.9 + 26.0
PROTEIN	Ctrl	107.5 + 10.4	110.0 + 13.2	104.3 + 13.5
	Fed	116.6 + 17.5	114.5 + 6.4	108.4 + 7.9
ASH	Ctrl	17.6 + 2.4	17.6 + 2.0	19.1 + 2.8
	Fed	17.0 + 0.7	17.9 + 2.5	17.8 + 3.2
INGESTA	Ctrl	40.7 + 15.4 **	17.0 + 8.8	49.7 + 18.1 **
	Fed	19.9 + 4.0 **	21.9 + 12.8	31.3 + 16.0 **

Data are mean ± 1 SD; sample sizes in parentheses at top of subsections (ctrl/fed).

*, $P < 0.05$; **, $P < 0.01$; from t-tests comparing control birds with supplementally-fed birds.

[a] A significant effect of food on laying female protein reserves was found in an analysis that included prelayers and postlayers (Table 5.2).

[b] A significant effect of food on incubating male fat reserves was found when incubation stage was controlled (Section 5.3.5, Fig. 5.4).

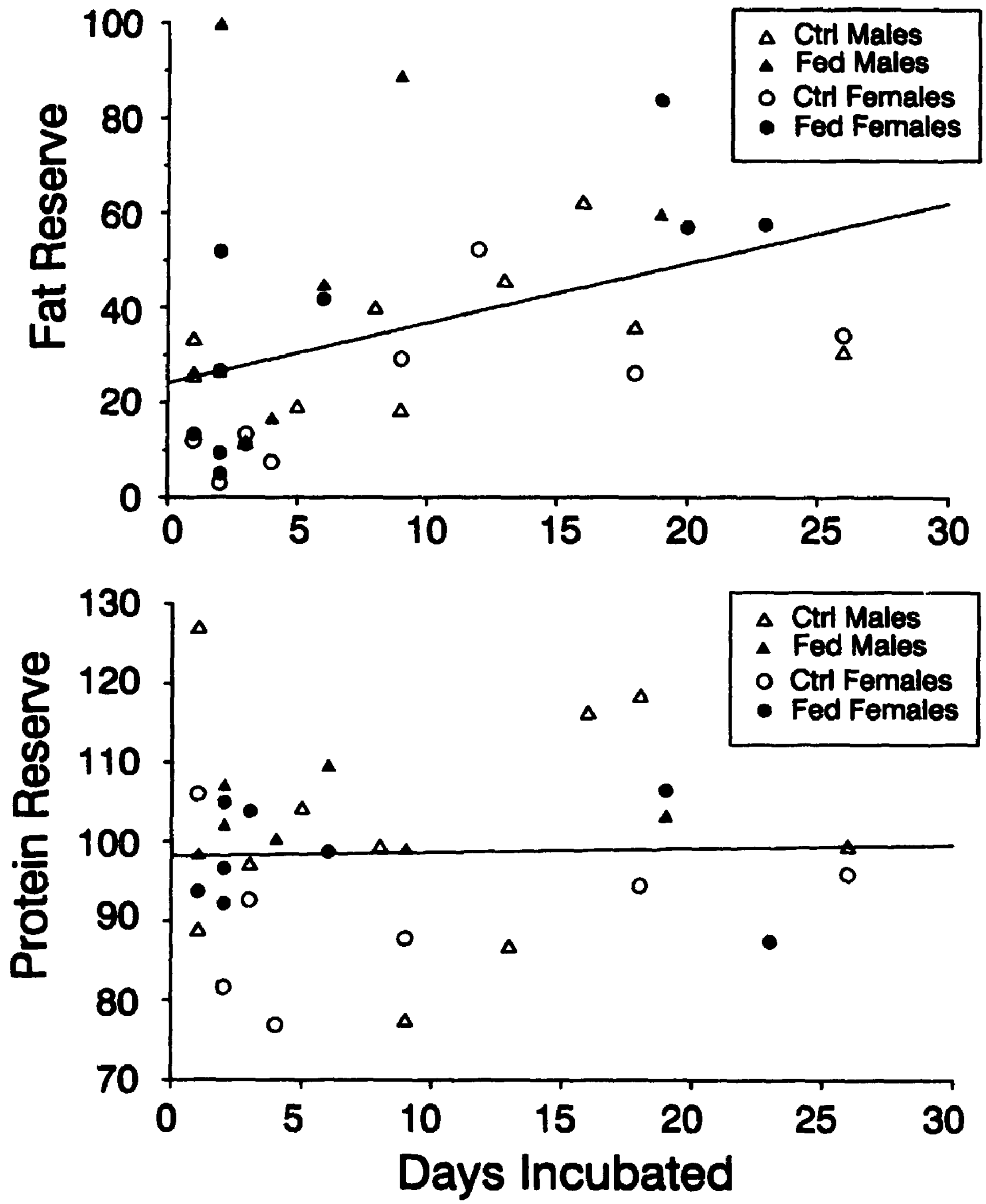


Fig. 5.4. Fat (top) and protein (bottom) reserves of male and female American Coots during incubation. Day 0 is the day of clutch completion, but effective incubation begins before then. Most nests have hatched at least some young by day 20. Protein reserves were corrected for structural size variation among all individuals of both sexes, hence significant sex effects (e.g., Table 5.1) are obscured. Trend lines are for all data (see text for discussion feeding effects).

Table 5.4. Factors affecting nutrient reserve dynamics of male and female American Coots during the brood-rearing period[a].

Effect:	Mass	Fat	Protein	Ingesta
Date	0.00, 0.98, --	12.33, 0.001, 0.83	4.71, 0.03, -0.83	5.51, 0.02, -0.41
Sex[b]	84.41, 0.0001, 140.1	1.65, 0.20, --	92.44, 0.0001, 24.8	7.57, 0.008, 11.9
Age[c]	8.70, 0.005, 26.9	0.03, 0.87, --	3.57, 0.06, --	1.01, 0.32, --
Food[b]	1.39, 0.24, --	12.39, 0.0009, 71.0	5.19, 0.03, 6.5	14.14, 0.0001, -17.6
Date * Sex	0.01, 0.94, --	1.39, 0.24, --	0.08, 0.78, --	1.09, 0.30, --
Date * Age	3.59, 0.06, --	0.35, 0.56, --	4.31, 0.04, 0.28	3.25, 0.08, --
Date * Food	0.15, 0.70, --	0.17, 0.69, --	0.02, 0.88, --	1.96, 0.17, --
Sex * Age	0.02, 0.90, --	0.05, 0.83, --	0.34, 0.56, --	0.62, 0.43, --
Sex * Food	0.34, 0.56, --	1.92, 0.17, --	0.22, 0.64, --	0.36, 0.55, --
Age * Food	0.27, 0.61, --	6.24, 0.02, -19.9	2.06, 0.16, --	1.08, 0.30, --

Note: data are F, P, and model coefficient (significant effects only). Analysis began with full model, nonsignificant effects were sequentially deleted based on examination of P values from Type III SS.

[a] Combined analysis of early and late brood-rearing stages.

[b] Coefficient direction for sex effect is Males > Females, and for food effect Fed > Ctrl.

[c] Age as indexed by tarsal color (Crawford 1978).

supplemental food (Table 5.4). This presumably was a reflection of the superior nutritional quality of food supplements in relation to natural foods (aquatic vegetation); i.e., supplementally-fed birds required less total food.

5.3.6 *Among-female variation in laying date, clutch size, egg size, and egg composition.*

Females with a pronounced bursa of Fabricius nested later than did females without a bursa, but clutch size was unrelated to this character (Table 5.5). However, timing of breeding was independent of female age as indexed by tarsal coloration (as was clutch size). Laying date and clutch size were largely independent of structural size measures (Table 5.5), only clutch size and keel length were significantly correlated ($r = -0.48$). In contrast, laying date was significantly negatively correlated with body mass, fat, and protein, and clutch size was significantly positively correlated with these same variables (Table 5.5). In all, 8 of 22 correlations (36%) involving laying date or clutch size were statistically significant at $P < 0.05$.

Egg size was insignificantly correlated with age and body mass (Table 5.5), multivariate structural size (i.e., canonical correlation of length, breadth, and volume *versus* wing chord, tarsus, culmen, and keel: $F_{(12,74)} = 1.44$, $P = 0.17$, $R^2 = 0.30$), and multivariate nutritional status of the laying female (canonical correlation of length, breadth, and volume *versus* carcass fat, carcass protein, carcass ash, and ingesta: $F_{(12,77)} = 1.50$, $P = 0.14$, canonical $R^2 = 0.26$). Egg volume was positively correlated with carcass protein (Table 5.5), but given the lack of significance in the multivariate tests, these correlations may be spurious.

Lipid and energy content of coot eggs were positively correlated with female age (as indicated by tarsus, but not by bursa), and yolk lean mass was positively correlated with female body mass (Table 5.5). Egg composition did not appear to be influenced by the structural size of laying females (canonical correlation analysis of albumen, yolk fat, and yolk lean versus wing chord, tarsus, culmen, and keel: $F_{(12,64)} = 1.21$, $P = 0.30$, $\underline{R}^2 = 0.37$; furthermore, only 2 of 30 (6.7%) simple correlations were significant at $\underline{P} < 0.05$). Yolk lipid was positively

Table 5.5. Simple Pearson correlations of laying date, clutch size, egg size, and egg composition with indices of age, body size, and nutrient reserves.

Female	Laying Date		Clutch Size		Egg Volume		Shell		Albumen		Yolk Fat		Yolk Lean		Protein		Energy	
trait:	r	P	r	P	r	P	r	P	r	P	r	P	r	P	r	P	r	P
Bursa	0.31	0.05	-0.23	0.37	-0.11	0.56	-0.37	0.24	-0.29	0.14	-0.15	0.44	-0.07	0.72	-0.23	0.23	-0.27	0.16
Age	-0.05	0.76	-0.03	0.90	0.27	0.11	0.23	0.39	0.24	0.16	0.43	0.009	-0.14	0.41	0.12	0.50	0.42	0.01
PC_{sex}	-0.01	0.97	0.23	0.37	-0.07	0.74	-0.29	0.36	-0.17	0.36	-0.19	0.28	0.02	0.90	-0.10	0.60	-0.24	0.19
Wing	-0.22	0.14	0.14	0.51	0.10	0.55	0.19	0.49	0.37	0.03	0.01	0.98	0.00	1.00	0.27	0.12	0.17	0.33
Tarsus	-0.06	0.69	0.29	0.16	0.14	0.41	0.38	0.14	0.11	0.52	0.12	0.49	0.01	0.96	0.09	0.63	0.10	0.56
Culmen	0.00	0.98	0.17	0.42	-0.23	0.17	-0.19	0.49	-0.33	0.05	-0.27	0.10	0.15	0.36	-0.14	0.41	-0.31	0.07
Keel	0.10	0.54	-0.48	0.05	-0.26	0.15	-0.39	0.21	-0.28	0.13	-0.21	0.25	-0.15	0.39	-0.26	0.16	-0.31	0.09
Mass	-0.33	0.02	0.48	0.02	-0.07	0.69	-0.38	0.15	0.06	0.74	-0.20	0.27	0.43	0.008	0.28	0.10	-0.04	0.80
Fat	-0.37	0.02	0.54	0.03	0.22	0.25	0.00	0.99	0.18	0.33	0.34	0.05	0.01	0.94	0.13	0.47	0.27	0.14
Protein	-0.33	0.04	0.66	0.004	0.38	0.05	0.32	0.31	0.15	0.43	0.23	0.21	0.36	0.04	0.29	0.12	0.25	0.17
Ash	-0.06	0.73	-0.15	0.56	-0.09	0.63	-0.11	0.74	0.03	0.86	-0.13	0.47	0.13	046	0.07	0.69	-0.10	0.60
Ingesta	-0.26	0.13	0.14	0.63	-0.32	0.08	-0.20	0.54	-0.04	0.83	-0.15	0.41	0.06	0.76	0.01	0.98	-0.22	0.55
Sample[a]	(40 - 47)		(17 - 24)		(36 - 43)		(12 - 16)		(28 - 35)		(28 - 35)		(28 - 35)		(28 - 35)		(28 - 35)	

[a] Samples sizes vary somewhat among variables. Some coots were measured live, hence they only contributed mass and structure data.

[b] Significant effects are underlined. No experiment-wise error rate was applied.

correlated with carcass lipid and yolk lean was positively correlated with carcass protein, but shell mass and carcass ash were independent. Egg composition was not related to variation in ingesta mass among females (Table 5.5).

In all, 3 of 84 correlations (3.6%) involving egg size or egg composition were significant at $P < 0.01$, and 8 (9.5%) were significant at $P < 0.05$ (Table 5.5). This suggests that at least some of these bivariate relationships may be real, despite the lack of significance in the multivariate tests. However, given the rather meagre significance levels, these "effects" should be viewed cautiously.

5.4 DISCUSSION

5.4.1 *Nutrient reserve dynamics of coots: general patterns throughout the breeding season.*

Nutrient reserves did not vary among general stages of the breeding cycle, except that fat reserves of male coots increased between early and late brood-rearing. This stability in body composition is in marked contrast to reserve dynamics just after the breeding season, when coots put on substantial quantities of fat (C. D. Ankney and T. W. Arnold, *unpubl. data*).

Some researchers have speculated that seasonal dynamics of body reserves might reflect endogenous annual rhythms, rather than alternating periods of nutritional excess and nutritional stress (e.g., Rohwer 1986*a*, Moreno 1989*d*). However, supplementally-fed coots were significantly fatter than unsupplemented coots in 5/6 comparisons (Table 5.3; the sixth comparison [late brood-rearing males] followed the same pattern, but not significantly so). Protein reserves were significantly higher in 3/3 comparisons of food supplemented *versus* unsupplemented females, and nonsignificantly higher in 3/3 comparisons involving males. This suggests that the "strategy" used by coots to regulate their body reserves during reproduction is decidedly more complicated than a simple series of seasonal set-points. In 2/3 comparisons involving males, ingesta mass was significantly lower in food supplemented birds, and in 3/3 comparisons involving females it was nonsignificantly so. Apparently, supplemented birds could meet their nutritional needs on less total food, as expected given the nutritional quality of food supplements as compared to natural foods (Appendix 1; Driver *et al.* 1974, Muztar *et al.* 1977). This is apparently the first study to demonstrate a significant effect of supplemental food on nutrient reserves, although several studies have reported changes in adult body mass associated with supplemental feeding (Newton and Marquiss 1981, Vaucoulon *et al.* 1985, Meijer *et al.* 1988, Brittingham and Temple 1989, Moreno 1989*a*, Hörnfeldt and Eklund 1990).

My results illustrate some potential dangers of using body mass to index changes in body condition through the breeding cycle. Although supplemental feeding did affect fat and protein reserves of breeding coots, there were no significant effects of feeding on body mass (Table 5.3), possibly due to reduced ingesta mass of food-supplemented birds, but also due to the generally low correlation between body mass and fat reserves among coots (Arnold, *unpubl. data*). Conversely, body mass exhibited significant changes between stages of the breeding cycle for females, but these changes were not attributable to changes in reserve size (they were probably due to enlargement and regression of the ovary and oviduct before and after egg-laying [e.g., Ricklefs and Hussell 1984], or to changes in ingesta content [Table 5.1]).

5.4.2 *Nutrient reserve dynamics of pre-breeding coots.*

Coots did not appear to acquire reserves after arriving on the breeding grounds, although this conclusion is somewhat tentative because new birds were still arriving on territories during the period when I was collecting pre-breeders (see Fig. 2.3), and I did not know how long birds had been at Minnedosa when they were collected. However, there were significant or nearly significant declines in protein reserves with collection date for both sexes, and declines in body mass and fat reserves among males. I suspect two possible causes for this variation: (1) better condition coots (including older birds; Alisauskas and Ankney 1985, Cavé et al 1989) are among the first arrivals, whereas subsequent arrivals are in poorer nutritional condition, and therefore mean nutrient reserves of the population decline with date even in the absence of changes within individuals, and (2) males take a much more active part in territory acquisition and defense (Ryan and Dinsmore 1979), and they therefore consume lipid reserves during peak periods of territory establishment.

Increases in nutrient reserves prior to nesting have been documented for Gadwalls (*Anas strepera*; C. D. Ankney and R. T. Alisauskas, *unpubl. MS*) and Canvasbacks (*Aythya vallisineria*; Barzen and Serie 1990), but were not observed in Blue-winged Teal (*Anas discors*; Rohwer 1986*a*). White-winged Scoters (*Melanitta fusca*; Dobush 1986) accumulated protein, but not fat, after arrival on the breeding grounds.

Because I did not want supplemental food to influence settling patterns of coots, food was not provided early enough in the season to affect body composition of pre-breeders. In retrospect, I wish that I had provided food very early on a few wetlands and had then collected birds to see if they stored nutrients prior to egg laying. Without such data, it is difficult to elucidate whether pre-nesting coots had no time or motivation to store reserves, or whether the availability of high-quality food was insufficient for them to have done so.

5.4.3 *Variation in nutrient reserves of egg-laying females.*

Contrary to Alisauskas and Ankney (1985), I found that nutrient reserves of female American Coots did not vary inversely with nutrients committed to reproduction. Several points seem worthy of comment:

1) Among controls, two of thirteen prelayers (15%) contained large amounts of fat (i.e., > 50 g), but no layers or end-of-layers (out of 31) contained more than 35 g of fat. Thus, females that initiated egg-laying with large amounts of fat appeared to utilize this reserve for clutch formation, but large fat reserves were not a prerequisite for breeding (c.f., Alisauskas and Ankney 1985).

Given the paucity of data from coots in late prelaying and early laying, it is possible that coots stored fat during rapid follicle growth, and then depleted this reserve during early egg laying (as in Canvasbacks, Barzen and Serie 1990). If this occurred, females would have had approximately 1 week to store and subsequently use these fat reserves. But, if females can store substantial quantities of body fat while simultaneously yolking follicles, it would appear that lipid cannot be that limiting.

2) Females that produced a small clutch always completed laying with minimal fat reserves, whereas females that produced a large clutch may or may not have depleted their fat reserves. This suggests that females producing small clutches (relative to the population mean) may have stopped laying because of nutrient shortages, but females producing large- or normal-sized clutches stopped laying in response to some other factor. As this conclusion is based on only 14 end-of-laying females, it must be regarded as tentative.

3) Among supplementally-fed coots, four of eleven layers (36%) contained appreciably more fat than the fattest control bird, yet on average fed coots laid only 0.8 more eggs than did controls and no fed birds laid a clutch larger than the largest control clutch. Hence, I was able to markedly manipulate size of nutrient reserves of some females through supplemental feeding, but this had little influence on clutch size. Supplementally-fed males attained even higher levels of fat storage during the laying period, suggesting that the nutrient demands of egg production may have prevented most females from using supplemental food to enhance their fat reserves during the laying period.

Based on these considerations, I reject the nutrient limitation hypothesis as a general explanation for clutch size limitation in the Minnedosa coot population. I concede that some females may use reserves during laying and that the clutch size of some females may be limited by the availability of reserves, but by and large, I conclude that most coots have little difficulty meeting the nutrient demands of clutch formation.

I also suspect that clutch size in the Delta Marsh coot population studied by Alisauskas and Ankney (1985) was not limited by nutrient availability, although I concede that Delta Marsh coots may have had more difficulty obtaining nutrients than did Minnedosa coots. Alisauskas and Ankney (1985) excluded two prelaying females from their analyses on the basis that these coots would not likely have bred; excluding these two birds inflated their estimates of reserve use by laying coots (although relationships were still significant with these two birds included; e.g., Alisauskas and Ankney 1985: Table 5). In my study, 10 out of 14 prelayers (71%) had lower fat reserves than Alisauskas and Ankney's estimated lower critical limit necessary for breeding (27.5 g). I obtained no evidence that females acquired reserves after arrival on the breeding grounds (Section 5.3.2), so either these birds laid normally using the reserves that they already had (and produced clutches that were, on average, larger than at Delta Marsh), or else they failed to breed (a conclusion that I regard as highly unlikely given that it would have affected approximately 70% of the population). Alisauskas and Ankney (1985: 142) conceded that some coots quit laying before depleting their nutrient reserves, and they speculated that territory quality affected clutch size by influencing the availability of exogenous reserves to the laying female. Although I agree that the availability of food on the territory can influence clutch size in coots (Chapter 3), it is not clear whether coots are proximately constrained by nutrient availability during laying, or whether they are using current food availability as an indication of future food availability during the brood-rearing period.

Although it is possible that the different patterns of nutrient reserve use (i.e., Alisauskas and Ankney 1985 *vs.* this study) represent real population differences, I remain suspicious. Sample size was smaller in the Delta Marsh study (n = 19 -21, *vs.* n = 57 in this study), and reproductive nutrients were based on assessment of post-ovulatory follicles (see Fig. 5.1) and average egg quality. Although Alisauskas and Ankney's sample included more females with small reproductive commitments (i.e., 2 - 10 g fat), this difference was not pronounced (n = 5 *vs.* n = 3 in this study). Finally, if their data are superimposed on mine, no qualitative differences are evident, except that several females in my study had lower fat and protein reserves than the lowest recorded in Alisauskas and Ankney's study (Fig. 5.5). The combined data also suggest that females may accumulate carcass fat during early follicle growth (e.g., Barzen and Serie 1990). If so, I interpret this as a temporary storage and retrieval strategy, such as that used by Brown-headed Cowbirds for calcium storage (Ankney and

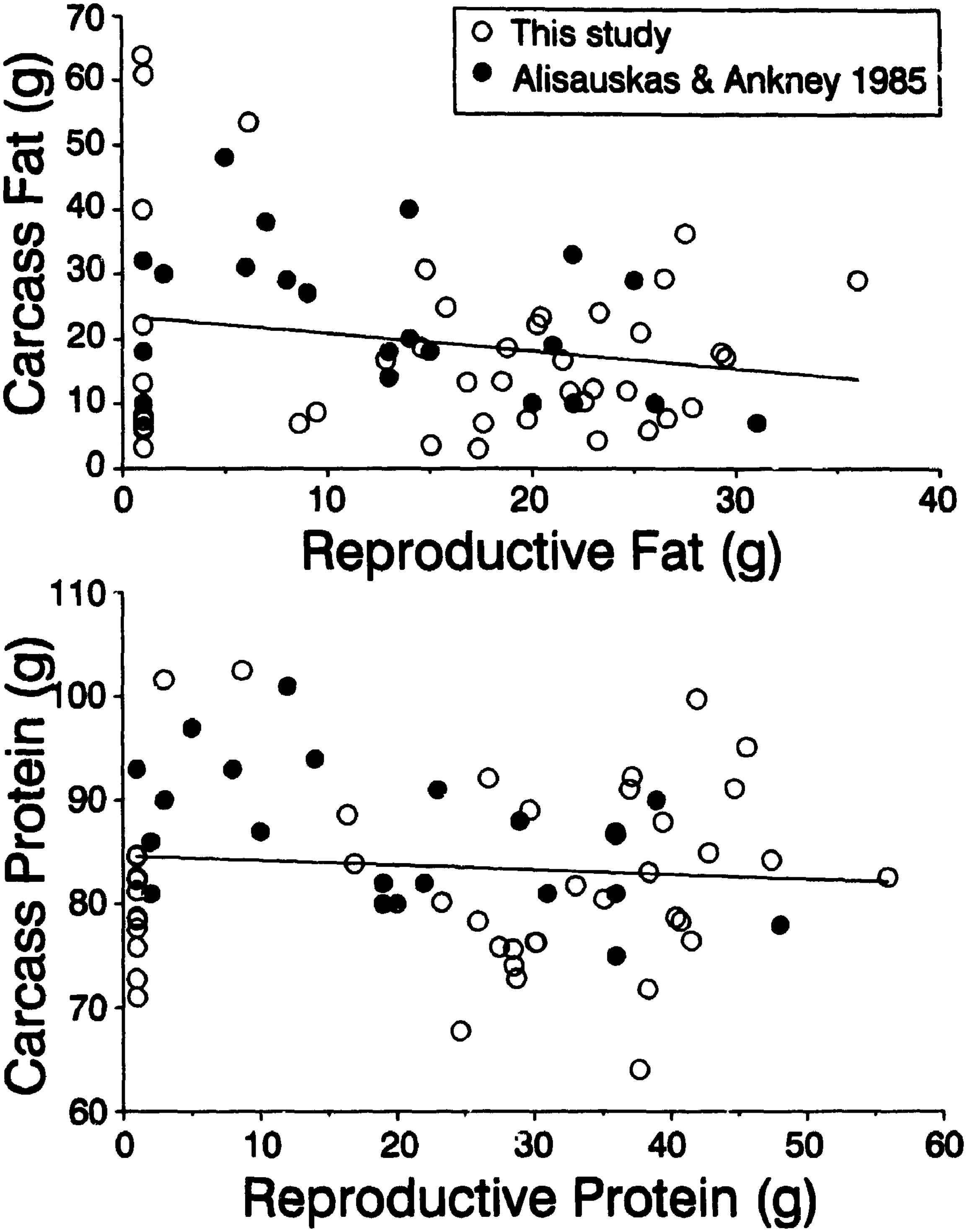


Fig. 5.5. Nutrient reserve dynamics of laying female American Coots based on two different studies: Alisauskas and Ankney (1985), Delta Marsh, Manitoba, and this study (Minnedosa, Manitoba). Minnedosa sample includes unsupplemented birds only.

Scott 1980), rather than an indication of nutritional super-abundance followed immediately by severe nutritional stress.

5.4.4 *Nutrient reserve dynamics of incubating coots.*

Coots exhibited no indication of negative energy budgets during incubation; in fact, fat reserves increased significantly throughout incubation. That fat reserves did not decline during incubation was not too surprising, given the reproductive system of coots. Most researchers have emphasized that incubation itself is not so rigorous (e.g., Walsberg and King 1978), rather the severe (or even complete) curtailment of foraging time constitutes the major cost of incubation (Ankney and MacInnes 1978, Afton 1979, Jones 1987, Moreno 1989*d*). Because both male and female coots incubate (Crawford 1977), each member of the pair has, on average, 12 hrs per day available for foraging (detailed attendance schedules of the two sexes have not been made, but both sexes engage in nocturnal and diurnal incubation; Crawford 1977; Arnold, *pers. obs.*). Thus, even though coots have to provide heat for large clutches, and nest in the same micro-environments as over-water nesting ducks, they do not mobilize fat or protein reserves to meet their maintenance energy requirements. Over-water nesting female waterfowl, on the other hand, are solely responsible for incubation and they often exhibit marked decreases in body mass during incubation (reviewed by Afton and Paulus *in press*).

As was the case during egg laying, supplementally-fed coots possessed larger fat reserves during incubation than did unsupplemented coots, and males possessed larger fat reserves than did females.

5.4.5 *Use of nutrient reserves during the brood-rearing period.*

Male fat reserves reached a seasonal low during early brood-rearing, whereas female fat reserves rebounded somewhat from the seasonal lows during laying and incubation. This was the only stage of the breeding cycle in which males and females had equivalent fat reserves (Table 5.1). This result was somewhat perplexing, because Ryan and Dinsmore (1979) and Horsfall (1984*a*, European Coots, *Fulica atra*) both showed that male coots contribute substantially less effort than do females towards feeding of young. During brood-rearing, male coots also spent more time in loafing and maintenance (i.e., preening) activities than did females (Ryan and Dinsmore 1979). However, males were more active than females in territory defense (repelling both intra- and inter-specific intruders) and they were primarily responsible for constructing brood platforms (Ryan and Dinsmore 1979). Perhaps these activities are more energy demanding than feeding newly-hatched young.

Fat reserves of males increased significantly throughout the brood-rearing period, suggesting that males experienced only temporary energy deficits during the earliest stages of brood-care. Fat reserves of females exhibited a smaller, nonsignificant increase during this time period.

On average, supplementally-fed birds had larger fat and protein reserves at the end of the brood-rearing period. Fed birds averaged 6.5 g more protein, and 17.4 g more fat, than did unfed birds.

5.4.6 *Among-female variation in laying date, clutch size, egg size, and egg composition.*

If presence/absence of the bursa is a reliable separator of yearlings and adults, then yearlings initiated nesting significantly later than older coots. This result was not confirmed, however, using tarsal coloration to index age classes. Structural size measures were largely independent of laying date, clutch size, and egg size (the few significant correlations that were observed were likely spurious). Relationships with nutrient reserves were apparent, however. Laying date was negatively correlated with body mass, fat, and protein, whereas clutch size was positively correlated with these traits. Egg size and lean yolk mass were positively correlated with body protein, and yolk fat was positively correlated with body fat.

Alisauskas *et al.* (1987) criticized this type of analysis because it compares breeding performance with nutrient reserve levels after the reserves are presumed to have been important (e.g., Murphy 1986*a*). I agree that failure to find correlations between reserve size and reproductive performance using this type of analysis cannot disprove that reserves are important. But, finding significant positive correlations does demonstrate at least two things: (1) that timing of breeding, clutch size, and egg size of coots are not regulated by population-level nutrient reserve "thresholds" (e.g., Reynolds 1972, Ankney and MacInnes 1978, Birkhead *et al.* 1983, Birkhead and Nettleship 1984, Alisauskas and Ankney 1985), and (2) that phenotypic traits that should exhibit either no correlation or a negative correlation under the egg formation hypothesis are, in fact, positively correlated among individuals. These data thus provide further evidence that clutch size in most coots is not limited by the availablility of nutrient reserves during egg production. At most, this limitation applies to those coots that produce relatively small clutches.

Although much of the variation in coot breeding performance seemed to be inherent within individuals, I suspect that the reason some individuals nested earlier and produced larger clutches of more nutrient-rich eggs was probably not because they were in better condition, or on better territories, than other coots (although they nevertheless were in better condition and on better territories). Rather, I suspect that there were "quality" individuals that were successful at all aspects of territory acquisition, breeding performance, and body maintenance, and there were also "inferior" individuals that were pretty much failures at whatever they attempted to do (e.g., Clutton-Brock 1988). Testing this hypothesis will be extremely difficult, but it will require experimentally manipulating food supplies and/or nutrient reserves downwards, rather than upwards. I know of only one attempt to manipulate food supplies downward among birds (an optimal foraging experiment with hummingbirds, with little relevance to breeding biology; Ewald and Carpenter 1978) and only two attempts among mammals (both on wintering populations; Todd and Keith 1976 *in* Boutin 1990, Bengtson *et al.* 1989); I cannot even conceive how one could non-invasively manipulate nutrient reserves downward.

Studies of nutrient reserve use by breeding birds are still at the descriptive stage. Although population- and species-level comparisons can suggest much about potential constraints on egg formation among groups of birds (e.g., Ankney and Alisauskas *in press*), we need better information on the consequences of nutrient reserves for individual birds (Ankney and Afton 1988), and we need experimental tests of the hypothesis that nutrient reserves are (are not) limiting the reproductive performances of individuals. In that vein, I hope that this work, and that of Rohwer 1986*a*, will serve as a useful beginning.

CHAPTER 6. SUMMARY AND CONCLUSIONS: FACTORS LIMITING CLUTCH SIZE IN AMERICAN COOTS

6.1.1 *Egg formation as a limiting factor.*

Overall, my data did not support the egg formation hypothesis as a general explanation for the adaptive significance of clutch size in American Coots (Table 6.1). Taken singly, most tests of this hypothesis were ambiguous, as there were usually always alternative explanations for any particular result (see Table 6.1). However, the weight of evidence (particularly the data on continuous laying) indicates that the egg formation hypothesis is inadequate for most nesting coots. I emphasize the word "most" because data on laying rates, and data on nutrient reserves of females that laid small clutches, both suggested that some females encountered problems in meeting the energetic demands of egg formation. I do not want to fall into the trap, as I believe David Lack did (e.g., Mayr 1973, Ydenberg and Bertram 1989), of seeking single, simple explanations for complex phenomena (Moreau 1944).

6.1.2 *Incubation capacity as a limiting factor.*

Fredrickson (1969) clearly demonstrated that American Coots were not limited by their ability to hatch larger than normal clutches. Indeed, Fredrickson could not even find an upper limit to clutch size based on incubation capacity, even though he manipulated some clutches to as high as 21 eggs, which was more than double the average clutch size in his study (X = 9.03 ± 2.01 [1 SD], range = 3 to 17; Fredrickson 1970). Most studies from other species of birds have also demonstrated that birds can successfully incubate more eggs than they typically lay (e.g., Lack 1947*b*, Morse and Wight 1969, Heusmann 1972, Clawson et al. 1979, Eriksson 1979, Slagsvold 1982, Rohwer 1985, Tarburton 1987, Baltz and Thompson 1988, Briskie and Sealy 1989). Winkler and Walters (1983) have suggested that incubation capacity is only likely to limit clutch size among species with sharply right-truncated clutch-size distributions (see also Lack 1947*a*). However, incubation capacity certainly does not limit Procellariformes to one-egg

Table 6.1. Summary of observational and experimental tests of the egg formation hypothesis of clutch-size (CS) limitation in American Coots.

	Does this test support the egg-formation hypothesis?		
Test:	Yes	No	Qualifying comments:
Annual variation in CS	*		1, 2
Seasonal decline in CS		*	1, 2
CS *vs.* egg size (ES) trade-offs: general		*	3
with supplemental food		*	4
in egg removal nests		*	4
in continuation nests		**	
CS *vs.* supplemental food	*		1, 5
CS variation among wetlands	*		1, 5
Laying rates *vs.* supplemental food	*		5
Laying rates in renest clutches	*		5
CS *vs.* egg removals		*	5
Renesting: propensity		*	
length of delay		*	
CS *vs.* initial CS		*	6
contintuation laying		***	
Egg composition: *vs.* CS		*	3
vs. supplemental food	*		5
Nutrient reserves: use during laying		**	7
response to supplemental food	*		8
vs. # developing follicles		*	9
vs. # of atretic follicles		*	9
vs. postlaying CS		*	1, 9, 10
vs. egg composition	*		1
OVERALL	*	***	

Notes: 1: other explanations likely, 2: food supply not measured, 3: variables not manipulated, 4: manipulations were weak, 5: effect not pronounced, 6: ignores seasonal decline, 7: few prelayers included, 8: reserves not used during laying, 9: small samples, 10: only part of population affected.

clutches (Rice and Kenyon 1962, Fisher 1968), Pelecaniformes to one- or two-egg clutches (Nelson 1964, Cash and Evans 1986), Columbiformes to two-egg clutches (Murton et al. 1974, Westmoreland and Best 1987), or Larinae to three-egg clutches (Winkler 1985, Reid 1987). Incubation capacity may limit Stercorariidae to two-egg clutches (Andersson 1976) and many shorebirds (Charadriidae and Scolopacidae) to four-egg clutches (Hills 1980; but see Shipley 1984), but this hypothesis is clearly inappropriate for most species of birds.

Experimental studies of the energetics of incubation have demonstrated that larger clutches require more energy to incubate (Biebach 1984, Haftorn and Reinertsen 1985, Weathers 1985, Moreno and Carlson 1989). In some species, this results in longer incubation periods (Baltz and Thompson 1988, Moreno and Carlson 1989, Smith 1989, Hepp *et al.* 1990; but see Rohwer 1985), presumably because eggs are not as well heated in large clutches. Incubation periods typically decline through the nesting season (Baltz and Thompson 1988, Moreno and Carlson 1989, Smith 1989, Hepp *et al.* 1990), either because eggs can better maintain heat during incubation recesses (due to higher ambient temperatures) or because more favorable feeding conditions for incubating parents result in fewer recesses (Moreno 1989c). In some of these studies, females increased their incubation constancy (% of time on nest), either through increased "courtship" feeding by their mates, or by losing body mass at a greater rate (e.g., Blagosklonov 1977 [*in* Jones 1987], Lyon and Montgomerie 1985, Jones 1987, Nilsson and Smith 1988, Moreno and Carlson 1989; but see Ankney and MacInnes 1978, Rohwer 1985). These studies suggest that hatching success should not be the only criterion by which the potential costs of incubating large clutches are measured.

In American Coots, the first-laid egg hatched one day sooner for each 10 day delay in clutch initiation ($P < 0.0001$), and approximately one day sooner among supplementally-fed coots *versus* unsupplemented controls ($P < 0.0003$; Arnold, *unpubl. data*). However, time-to-hatch of the first-laid egg was independent of clutch size (number of eggs laid by the female; $P = 0.43$), incubated clutch size (different from the previous measure in 58/125 nests due to experimental egg transfers, nest parasitism, or partial clutch losses; P = 0.95), and nesting attempt (initial clutches *versus* renests *versus* continuation nests; P = 0.73) (Arnold, *unpubl. data*). Moreover, most coots appeared to accumulate fat reserves during incubation (Chapter 5). These observations suggest that incubation costs can be safely dismissed as an explanation of clutch-size limitation in American Coots.

6.1.3 *Brood-provisioning as a limiting factor.*

Overall, the results from brood-manipulation experiments provided little general support for Lack's (1947*a*) brood-provisioning hypothesis (Chapter 1), although his predictions were certainly supported by some studies (i.e., 21% of the studies cited in Table 1.1). Perhaps coots are among the ranks of birds that cannot rear more offspring than normal.

Ryan and Dinsmore (1979) showed that time budgets of female American Coots were severely constrained during brood rearing, with almost all available time devoted to feeding (offspring and themselves). However, this high level of investment was not maintained for very long (ca. 20 d total, 6 d maximal; Ryan and Dinsmore 1979: Fig. 1). Males, on any given day during brood-rearing, contributed only about half as much effort towards feeding offspring as did females (Ryan and Dinsmore 1979). This suggests that if fledging success is constrained by brood provisioning, then reproductive output could be increased by a factor of 1.3 if males would increase their feeding rates to levels observed among females. Oddly, I found that male coots were in poorer body condition than females during early brood-rearing (Section 5.3.5), and that females seemed to be more likely to desert the brood to initiate early wing molt (C. D. Ankney and T. W. Arnold, *unpubl. data*). Whether higher feeding rates of females represent a cause, or a consequence (or perhaps neither), of earlier brood abandonment represents an interesting and unresolved question. However, lower parental investment by males appears to be commonplace among typically monogamous birds (e.g., Møller 1988, Bart and Tornes 1989, Slagsvold and Lifjeld 1990; but see Beissinger 1987), perhaps due to uncertainties of paternity, and thus its occurrence among male coots may not require a unique explanation.

I conducted preliminary tests of the brood-provisioning hypothesis in coots by experimentally manipulating brood sizes and food availability. Only one investigator (Crossner 1977) has experimentally manipulated both of these variables and critically tested Lack's hypothesis in full; i.e., that parents cannot, on average, rear more young than normal, and the reason they cannot do so is due to food availability. Crossner (1977) verified that food was important in determining nestling growth rates and fledging success in European Starlings (*Sturnus vulgaris*) (see also Magrath 1989, Dhindsa and Boag 1990, Simons and Martin 1990), but he also showed that parents could rear about one more young than average without supplemental food (Power *et al.* [1989] provide an explanation for Crossner's results which is consistent with Lack's hypothesis, though I find it a bit farfetched).

My attempts to test the brood-provisioning hypothesis in 1988 resulted in rather meagre data, and in the 1989 drought season I obtained no relevant data at all. Consequently, I decided to defer this topic from formal presentation (i.e., as a thesis chapter). Preliminary analyses suggested that fledging success, growth rates, and body condition were higher among supplementally-fed broods, but there were no demonstrable effects of brood size or hatching order on these variables (Tables 6.2 and 6.3, Figs. 6.1 and 6.2). These data indicate that food availability can be an important determinant of fledging success in coots, but in the absence of brood-size effects, they do not support Lack's hypothesis of clutch-size determination (neither do they constitute very strong rejection of his hypothesis).

Other investigators have reported a high degree of brood reduction among newly-hatched coots (including both American and European coots), suggesting that brood size might be constrained by parental feeding abilities (Horsfall 1984*a,b*, Hill 1988, Lyon *in press*). For coots, testing Lack's brood-provisioning hypothesis for clutch size will therefore necessitate testing his brood-reduction hypothesis for hatching asynchrony (Lack 1947*a*), because clutch size and hatching asynchrony are inextricably confounded in coots. As was the case for the brood-

Table 6.2. Effects of food supplementation, brood size, and hatching order on recapture rates (i.e., a survival index) of 179 fledged American Coot chicks[a].

Effect:	Parameter[b]	df	χ^2	P
Intercept	1.28	1	46.53	0.0001
Food	0.44	1	5.51	0.02
Brood Size (BS)	.--	1	1.90	0.17
Hatch Order (HO)	.--	1	1.60	0.21
Food * BS	.--	1	1.67	0.20
Food * HO	.--	1	0.04	0.85
BS * HO	.--	1	0.60	0.44
Food * BS * HO	.--	1	2.71	0.10

[a] Data analyzed with logistic regression (PROC CATMOD, SAS Institute Inc. 1985). Nonsignificant effects were sequentially deleted beginning with highest-order interactions.

[b] Only significant parameters are presented. Survival increased with food availability (38.8% recapture rate with supplemental food, 16.3% without supplemental food).

Table 6.3. Effects of food supplementation, age, and hatching date on body mass and tarsus length of fledgling American Coots (n = 41 marked known-age chicks).

	Body Mass			Tarsus Length		
Effect:	F	P	b	F	P	b
Age	0.35	0.56	--	5.11	0.03	0.02
Food	4.18	0.05	53.2	5.35	0.03	-17.51
Hatch Date (Date)	2.63	0.11	--	0.30	0.59	--
Age * Food	0.30	0.59	--	6.47	0.02	[illegible]5[a]
Age * Date	1.98	0.17	--	0.76	0.39	--
Food * Date	0.84	0.37	--	0.67	0.42	--
Age * Food * Date	1.76	0.19	--	0.98	0.33	--

Notes: Nonsignificant effects sequentially deleted from statistical model based on examination of Type III SS. Coefficients are given for significant effects only. Coefficients for Food effect are Fed > Ctrl.

[a] Fed chicks have larger Tarsus after 49 d of age. Mean age of chicks in sample was 50.4 d (range 36 - 65).

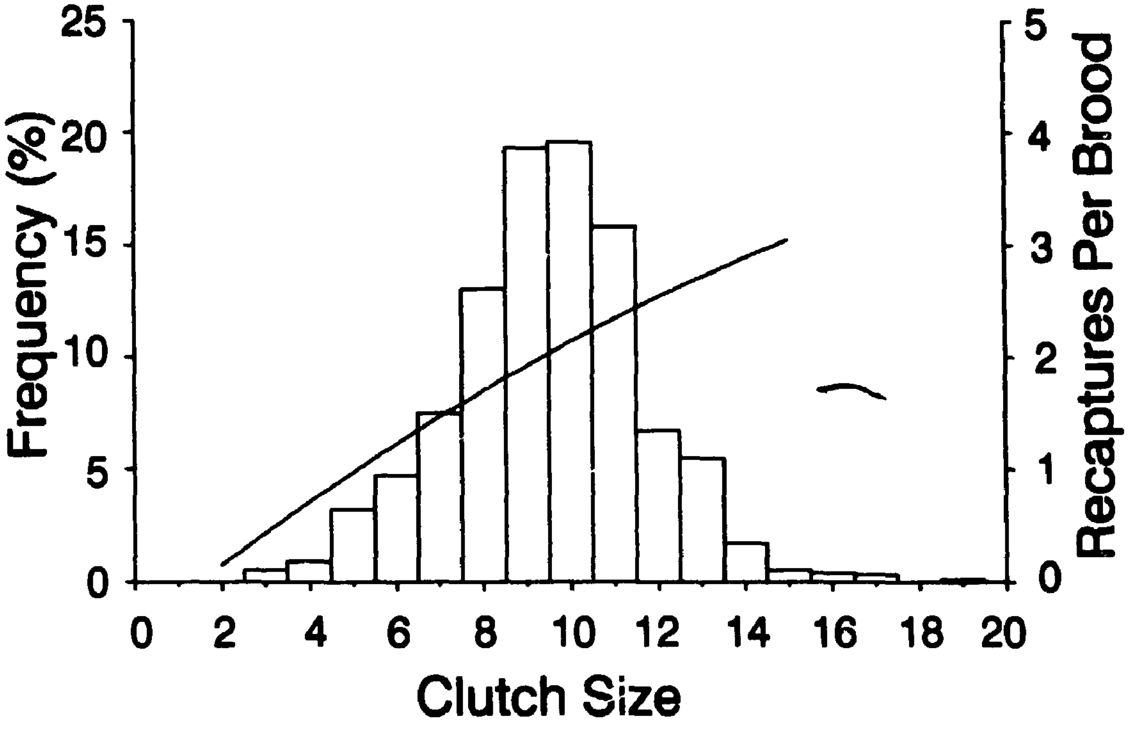


Fig. 6.1. Fledging success as a function of brood size (the slightly curvilinear line) in relation to the frequency distribution of clutch size in the Minnedosa coot population. The relationship for fledging success versus brood size is a quadratic line of best fit for 48 broods with experimentally manipulated brood sizes (-4, 0, +4 eggs removed from/added to the clutch just before hatch), but the relationship is not significant. Fledging success was determined at 36 - 65 d of age, long after chicks were independent of parental feeding (e.g., Ryan and Dinsmore 1979).

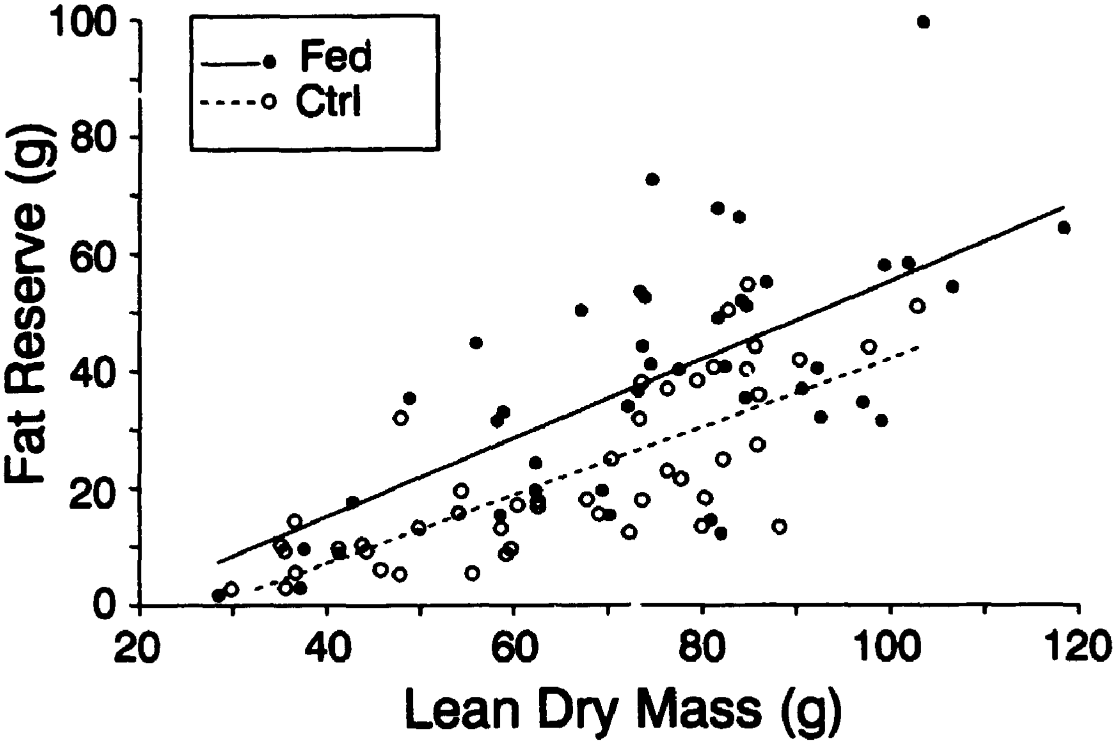


Fig. 6.2. Fat reserves of American Coot chicks in relation to body development (lean dry mass) and supplemental feeding. Feeding effect is highly significant (F = 14.30, P = 0.0003) and feeding * lean dry mass effect is nearly significant (F = 2.95, P = 0.09).

provisioning hypothesis, Lack's brood-reduction hypothesis has not been generally supported by experimental data (reviewed by Amundsen and Stokland 1988; but see Magrath 1989), and it is therefore unclear whether brood reduction in coots represents a cause, or a consequence, of asynchronous hatching (e.g., Clark and Wilson 1981; see beyond).

6.1.4 *The cost of reproduction.*

There was little evidence that adult coots were under nutritional stress during any specific stage of the breeding cycle, although fat levels were generally low throughout the entire season (Table 5.1). If body reserve dynamics are an accurate indicator of reproductive stress (e.g., Yom-Tov and Hilborn 1981, Nur 1984*b*; but see Moreno 1989*d*), then my data provided little evidence that breeding American Coots are incurring substantial costs during egg-laying, incubation, or brood-rearing (although adult males had little fat during early brood-rearing, they had attained their highest seasonal fat levels by late brood-rearing). Coots are capable of putting on enormous fat deposits in preparation for fall migration (C. D. Ankney and T. W. Arnold, *unpubl. data*), so perhaps coots remain lean throughout the summer simply because it is more efficient not to be burdened down by unnecessary body fat (e.g., Freed 1981, Norberg 1981).

Among female coots, fat reserves of non-breeders were higher than those of breeders (Arnold, *unpubl. data*). I suspect that non-breeders are of inferior overall quality, relative to breeders (i.e., age, body size, foraging capacity; see Alisauskas 1987), so their larger fat reserves are somewhat perplexing. Bailey (1985) attributed a similar pattern of variation in protein reserves of breeding and non-breeding male Redheads (*Aythya americana*) to energetic costs of reproduction, but such costs seem difficult to ascribe to coots given that egg-laying and incubation did not deplete reserves (Chapter 5). Perhaps there is an overall cost associated with breeding (i.e., maintaining a territory) such that breeders have lower reserves than non-breeders. Alternatively, non-breeders may have a different strategy of maintaining nutrient reserves, relative to breeders.

I obtained no evidence of intraseasonal costs of reproduction among renesting coots. Renesting propensity, delay, clutch size, and egg size were unaffected by past investment in egg laying or incubation. It seems intuitively obvious that costs of reproduction would be more likely to manifest themselves soon after a breeding event than at some distant time in the future. Indeed, much of the best evidence for costs of reproduction in passerine birds are for intraseasonal, as opposed to interseasonal, costs (Kluyver *et al.* 1977, Smith and Roff 1980, McGillivray 1983, Slagsvold 1984, Finke *et al.* 1987, Linden 1988, Smith *et al.* 1987, Boer-Hazewinkel 1987, Hegner and Wingfield 1987, Tinbergen 1987, Orell and Koivula 1988; cf. DeSteven 1980, Smith 1981, Boyce and Perrins 1987, Pettifor *et al.* 1988; but see Askenmo 1979, Bryant 1979, Røskaft 1985, Nur 1988*a,b*, Gustafsson and Sutherland 1988). Given that coots often exhibit rather poor philopatry to a specific breeding area (see Figs. 2.1 and 2.3), evaluation of interseasonal costs of reproduction among coots will be difficult, if not impossible. Møller (1989) has expressed concern that too much of our knowledge of avian life-histories is based on birds that breed in rectangular wooden boxes set out in rectangular study grids; given that 16 of the 20 studies referenced above are from box-nesting birds, his concern is perhaps well-founded (see Section 6.1.7).

6.1.5 *The nest predation hypothesis.*

Lack (1948*a*) recognized large differences in clutch size between open-nesting and cavity-nesting European birds (see also Moreau 1944), which he attributed to differences in predation rates. Lack (1948*a*) reasoned that parent birds could use the same amount of food to raise a few young quickly (i.e., rapid growth) or several young more slowly, but only birds with secure nest-sites could afford the luxury of long, vulnerable nestling periods. The predation hypothesis applies not only to the length of the nestling period, but also to the egg-laying period. By laying additional eggs, females expose their clutch to predators for a longer period of time, because each egg takes a day or more to produce and hatch is thus delayed by a corresponding interval (Perrins 1977). Most researchers have dismissed the nest predation hypothesis as being trivial (e.g., Lack 1947*a*, Johnsgard 1973, Perrins 1977, Ricklefs 1977, Winkler and Walters

1983), but several recent authors have demonstrated that nest predation could have an important modifying effect on optimal clutch size (Slagsvold 1982, Lundberg 1985, Arnold *et al.* 1987, Milonoff 1989, Martin *in press*). Lima (1987) suggested that predation on breeding adults while they were foraging could also have an important influence on optimal clutch size of nidicolous birds, and this effect would be almost impossible to detect in field studies (Lima studied this "effect" with a computer simulation).

Nest predation appears unlikely to have an important effect on optimal clutch size in coots because nest predation rates are generally very low (ca. 15% in 1988; Arnold, *unpubl. data*). Furthermore, coots hatch their eggs asynchronously and young can exit the nest within hours of hatching. As a result, nest contents are not exposed to greater predation risk if clutch size is increased. Hussell (1972, 1985) and Clark and Wilson (1981) have suggested that hatching asynchrony has evolved precisely because of this ameliorating effect on nest predation, and not to facilitate brood reduction as proposed by Lack (1947*a*, 1954, 1968). The fact that asynchronous broods almost invariably fledge fewer young than experimentally-synchronized broods (reviewed in Amundsen and Stokland 1988) lends considerable support to Hussell's hypothesis. Given that hatching asynchrony may actually reduce fledging success, then the nest predation hypothesis is perhaps relevant to coots after all.

6.1.6 *The egg-viability hypothesis.*

Arnold *et al.* (1987) hypothesized that clutch size in prairie dabbling ducks was limited by the length of time that eggs could remain viable in an unincubated nest. Because ducks hatch their eggs in synchrony and exit the nest *en masse* soon after hatch, they cannot maintain egg viability by initiating incubation during egg laying, or else they would disrupt the developmental synchrony of their embryos (but see Arnold *et al.* 1987 for additional complicating details). Among coots, however, egg viability would not seem to be important because parents can begin incubation during egg laying (and, in fact, they do; Arnold, *unpubl. data*).

I measured rate of decline in egg viability during my 1987 and 1988 field seasons. Viability declined sharply (Fig. 6.3), much more strongly than in ducks. If egg viability declines are combined with nest predation costs (after Arnold *et al.* 1987), an optimal clutch size of 11 is predicted, assuming that coots postpone incubation until after clutch completion and that no other costs influence clutch size. By hatching their young asynchronously, however, these costs can be obliterated (Fig. 6.4). Thus, determining whether the nestling hierarchies that arise from early incubation onset are in fact adaptive, as Lack (1947*a*) suggested, or maladaptive, as Clark and Wilson (1981) maintain, is a crucial objective to understanding the adaptive significance of clutch size in coots.

6.1.7 *Some thoughts about nest-sites.*

As mentioned earlier, Lack (1947*a*) attributed the larger clutch sizes of hole-nesting European birds to their greater security from nest predators. Similar variation in clutch size with respect to nest-site has been documented for the African, Neotropical, and Nearctic avifaunas (Moreau 1944, Skutch 1985, Kulesza 1990). Lack (1954), Nice (1957), and Ricklefs (1969), among others, have summarized evidence that nest success is higher among cavity-nesting birds, but much of this data is derived from nest-box studies, rather than natural cavities (see Møller 1989). Kulesza (1990) demonstrated, in a comparative study of New World passerines, that nest-site affected clutch size <u>after</u> controlling for variation in predation rates. In a variety of nest-box studies, clutch size has been positively correlated with size of the nest box (Karlsson and Nilsson 1977, Eriksson 1979, van Balen 1984), and this relationship has recently been verified among populations nesting in natural cavities (Rendell and Robertson 1989). Slagsvold (1982, 1989*a*) and Westmoreland and Best (1987) have demonstrated, by experimentally manipulating nest-bowl size, that fledging success in open-nesting birds also increases with nest size. These observations suggest that physical crowding of eggs and/or chicks might limit clutch size (see also Martin 1988*a*), but such an hypothesis begs the question "Why don't birds build bigger nests?" Slagsvold (1989*a,b*) reviewed several hypotheses and suggested that predation rates might increase with nest size (and conspicuousness), or that large nests

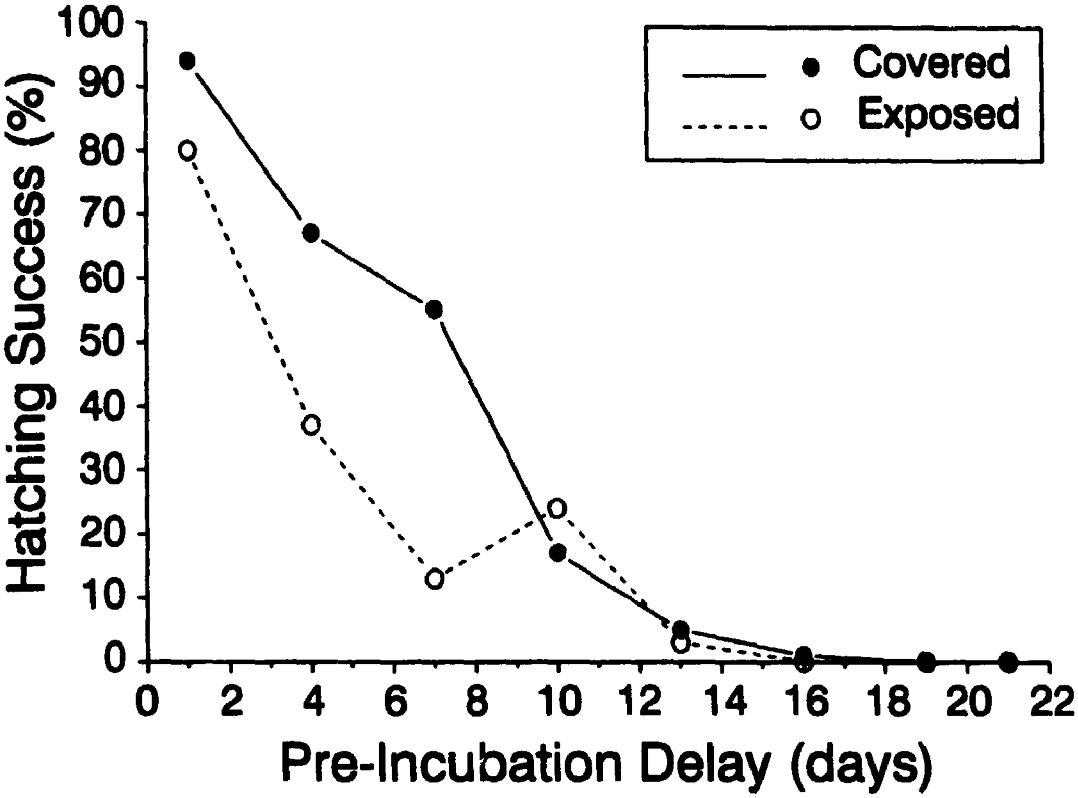


Fig. 6.3. Hatchability of 311 American Coot eggs in relation to experimental pre-incubation delay. Data were pooled by 3 day intervals to minimize random daily fluctuations. Incubation was delayed by placing eggs in artificial over-water coot nests. Eggs were then returned to active coot nests for natural incubation. Decline in viability with increasing delay was highly significant ($P < 0.0001$), with no eggs hatching after 14 d delay. In early stages of delay, hatchability was maintained somewhat ($P < 0.05$) by shielding eggs from solar radiation with four layers of burlap. However, even among "covered" eggs, viability decline is much more pronounced than for dabbling ducks (Arnold *et al.* 1987). I conclude that coots cannot afford to postpone incubation onset until after clutch completion.

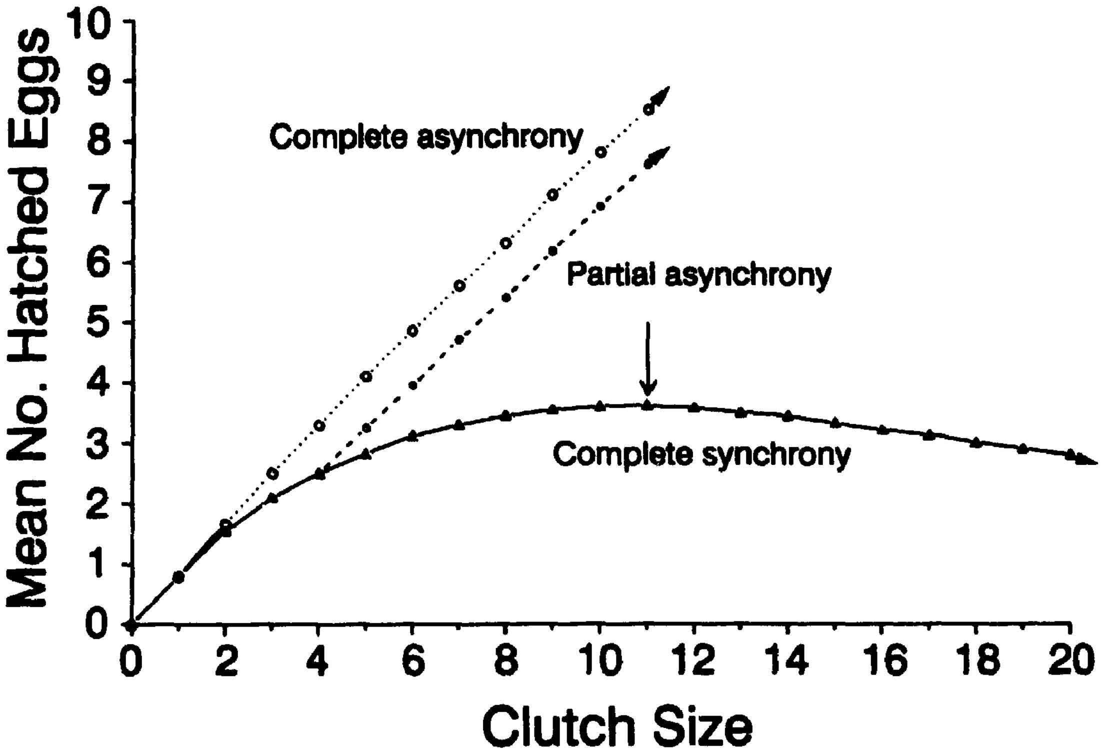


Fig. 6.4. Estimated mean number of eggs hatching from different sized coot clutches as a function of egg viability, nest predation, and incubation strategy. With complete hatching synchrony, coots derive no benefits from laying more than 11 eggs (as indicated by the arrow above the lower curve). Hatching success is maximized for total asynchrony, but no coots exhibit this pattern (Arnold, *unpubl. data*). The most common incubation strategy, partial asynchrony, is indicated by the middle line. Most coots begin incubation between the third to sixth laid egg (Arnold, *unpubl. data*).

might result in less efficient incubation (Martin 1988*a* suggests a similar hypothesis to explain differences between elevated- and ground-nesting passerines). Variations in clutch size among local nest-sites are unlikely to be related to food availability, because birds are not necessarily foraging where they nest (e.g., Martin 1988*a*; see also Alerstam and Högstedt 1981). Recent conjecture suggests that nest-sites might influence several factors not usually regarded as breeding adaptations, such as winter-residency patterns (Alerstam and Högstedt 1981), male and female plumage characters (Stutchbury and Robertson 1987, Martin 1988*a*), and even avian community structure (Martin 1988*b*) and social systems (Ligon *et al.* 1988). Given the overwhelming evidence that clutch size varies among nest-sites, and the rather paltry evidence that clutch size is affected by food supply (e.g., Hussell and Quinney 1987, Daan *et al.* 1988), one has to wonder if Lack (1948*a*) made a major error in judgement when he assigned the "nest-site effect" to the modifying role.

Because the "nest bowl" for hatchling coots is the surrounding wetland, rather than the actual nest bowl where the clutch was incubated, nest size constraints are essentially eliminated during brood rearing, and so, apparently, is sibling competition for parental feedings. Among most nidicolous birds, food is brought to the nest and distributed largely according to "demand" behavior (Bengtsson and Rydén 1983, Hussell 1988), and older nestlings can effectively monopolize access to food (Bengtsson and Rydén 1983, Ploger and Mock 1986). But among coots, moorhens, and grebes, parents effectively regulate which chicks can obtain feedings (Horsfall 1984*a*, Desrochers and Ankney 1986, Forbes and Ankney 1987, Leonard *et al.* 1988), and such parental control over feeding rates may effectively negate any disadvantages normally experienced by late-hatching chicks. If so, the causes and consequences of hatching asynchrony in coots (as well as moorhens and grebes) may be radically different from those of "typical" nidicolous birds.

6.1.8 *So what limits clutch size in American Coots?*

I must confess that I have no ready answer to a question that has already consumed three major and three minor field seasons, not to mention quite a lot of paper. Most of my effort has been expended at testing the egg formation hypothesis advanced by Alisauskas and Ankney (1985), and I believe that it can now be safely removed from the list of competing hypotheses. Fredrickson (1969) previously eliminated the incubation capacity hypothesis, and nothing in my research indicated any reason to revive it. The brood-provisioning hypothesis remains viable and largely untested. Future research on clutch-size determination in coots will have to overcome the many logistical problems associated with this hypothesis, and put it to critical test. The adaptive significance of hatching asynchrony in coots will have to be addressed concurrently. Until these tasks are completed, any claims that reproductive rates in American Coots are or are not related to food availability will be premature, and more than likely, wrong.

APPENDIX 1. NUTRITIONAL CONTENT OF SUPPLEMENTAL FOODS

A1.1 *Steam-rolled corn, Cargill Ltd., Brandon, Man.*

Dry matter, 50%; crude protein, 10.9% of dry weight; crude fiber, 2.4% of dry weight; ash, 1.6% of dry weight; ether extract, 4.7% of dry weight; nitrogen-free extract, 80.4% of dry weight (Alisauskas *et al.* 1988).

A1.2 *Trout chow, Martin Feed Mills Ltd., Elmira, Ont.*

Martins 84G Grower Pellets for Salmonids, guaranteed analysis: crude protein, ≥ 40.0%; crude fat, ≥ 10.0%; crude fiber, ≤ 3.0%; Vitamin A, ≥ 7500 iu/kg; Vitamin D_3, ≥ 300 iu/kg; Vitamin E, ≥ 100 iu/kg; ascorbic acid, ≥ 800 mg/kg.

A1.3 *Layer diet (for chickens), Federated Co-operatives Ltd., Saskatoon, Sask.*

Co-op Layer Diet 20, guaranteed analysis: crude protein, ≥ 18.0%; crude fat, ≥ 3.0%; crude fiber, ≤ 5.0%; calcium, 3.060%; Phosphorus, 0.60%; Sodium, 0.16%; Vitamin A, ≥ 10,500 iu/kg; Vitamin D_3, ≥ 1850 iu/kg; Vitamin E, ≥ 15 iu/kg.

A1.4 *Rabbit pellets, Nutrena Feeds, Cargill Ltd., Winnipeg, Man.*

Nutrena Bunny Booster, guaranteed analysis: crude protein, ≥ 18.0%; crude fat, ≥ 3.0%; crude fiber, ≤ 13.0%; calcium, 1.25%; phosphorus, 0.80%; sodium, 0.20%; Vitamin A, ≥ 10,000 iu/kg; Vitamin D_3, ≥ 2500 iu/kg; Vitamin E, ≥ 50 iu/kg.

A1.5 *Chick starter, Federated Co-operatives Ltd., Saskatoon, Sask.*

Co-op Chick Starter - 18%, guaranteed analysis: crude protein, ≥ 18%; crude fat, ≥ 2.0%; crude fiber, ≤ 6.0%; sodium, 0.16%; calcium, 0.9%; phosphorus, 0.7%; Vitamin A, ≥ 8600 iu/kg; Vitamin D_3, ≥ 1500 iu/kg; Vitamin E, ≥ 20 iu/kg; medicated with amprolium 0.0125%; selenium, 0.100 mg/kg.

APPENDIX 2. IDENTIFICATION OF INDIVIDUAL AMERICAN COOTS BASED ON EGG CHARACTERISTICS

A2.1 RATIONALE

Studies of renesting and multiple-brooding in birds have generally been based on intensive observations of individually color- or radio-marked birds (e.g., Doty *et al.* 1984, Rohwer 1986*a*, Arcese and Smith 1988). In 1988 in a preliminary attempt to study renesting in American Coots, I nest-trapped (e.g., Crawford 1977) and leg-banded 5 coot pairs during early incubation and then removed their clutches. In 4 of 5 cases, suspected renests were initiated within 10 days and within 20 m of the original nests, but the birds had become trap-shy and I was unable to recapture them for positive identification. Only later did I learn that previous researchers have used external egg characteristics to identify subsequent nesting attempts by individual birds (e.g., Thompson *et al.* 1986).

Studies of intraspecific nest parasitism require that investigators can reliably distinguish nests that have been parasitized and/or eggs that have been laid parasitically. Researchers have used a variety of cues to accomplish this, including direct observation of parasitic events (Brown and Brown 1988); super-normal clutch sizes or laying rates (Young and Titman 1988, Rohwer and Freeman 1989); new eggs appearing during incubation or, for nests first discovered after the parasitism event, pronounced developmental asynchrony within clutches or broods (Young and Titman 1988, Bryant and Tatner 1990); differences in size, shape, color, and/or markings among eggs (Yom-Tov 1980, Gibbons 1986); examination of postovulatory follicles in collected birds (Kennedy *et al.* 1989); administration of trace compounds (Haramis *et al.* 1983); protein electrophoresis (Romagnano *et al.* 1989); and DNA fingerprinting (Quinn *et al.* 1987). However, many of these techniques are labor intensive, destructive, or financially inhibitive. Perhaps the most efficient technique for identifying parasitized nests is to monitor laying rates with frequent nest visits (Rohwer and Freeman 1989). During my work with coots, I detected fairly high rates of intraspecific nest parasitism, as evidenced by super-normal laying rates (Arnold, *unpubl. data*). Because a major topic of my research was clutch-size determination (see Chapter 3), I wished to exclude parasitic eggs when measuring clutch size. But because many nests were visited infrequently (e.g., every 6 days during 1988), it was not possible to identify all parasitically laid eggs based on laying rate information (see also Frederick and Shields 1986). At nests that I knew had been parasitized, based on laying rate information, there were often pronounced differences in egg appearance. Further qualitative examination of coot clutches showed that egg appearance was highly consistent within clutches, but fairly variable among clutches, suggesting that egg appearance might be sufficient for recognizing parasitic eggs. Two recent papers have sought to assess inter-female variation in egg appearance using a variety of detailed semi-quantitative methods (e.g., Brown and Sherman 1989, Thomas *et al.* 1989). While such efforts are admirable, and perhaps even useful, I did not take this detailed quantitative approach because such a labor-intensive system would have precluded its usefulness in my research. Instead, I assessed eggs by examining them, side by side, and asking "Are they similar, or are they different?". To evaluate the merits of such an admittedly subjective approach, I conducted the following experiments to assess the effectiveness of qualitative examination of external egg characteristics for identifying individual female coots.

A2.2 MATERIALS AND METHODS

Partial and complete coot clutches were obtained from nests that I had collected as part of a renesting experiment, from nests that had been abandoned for unknown reasons, or from eggs that I had candled and found infertile. Only nests that I had visited several times during laying and was reasonably sure had not been parasitized were used as sources. In all, 171 eggs from 61 different clutches were available for identification trials; however, many of these clutches provided only 1 or 2 eggs and could only be used as potential "parasitic" eggs. Twenty-one clutches provided enough eggs to serve as "host" clutches in the following experiments. Eggs were individually marked with nest and egg numbers using black permanent ink (Sharpie) on the apex of the egg. Eggs were placed in commercial egg flats (resembling grocery store egg cartons) during identification trials and only the tops and upper sides of eggs were visible; egg numbers were not seen until after the experiments were over.

Experiment 1.--In this experiment, I was presented with a tray containing 6 sets (clutches) of 3 eggs and a single unmatched egg that was from the same clutch as 1 of the 6 sets. After visually examining the external characteristics of the single egg and the 6 sets of eggs, I selected the set of eggs that I believed the single egg belonged to.

Experiment 2.--Experiment 2 resembled Experiment 1 in all ways except that there was a 50% chance that the single unmatched egg did not belong to any of the 6 sets.

Experiment 3.--I was presented with 4 eggs, 3 of which were from the same clutch and 1 of which was a "parasitic" egg randomly selected from all other available eggs. Based on visual examination, I selected the egg that I believed was parasitic.

Experiment 4.--This was identical to Experiment 3, except that there was a 50% chance that there would not be a "parasitic" egg (all 4 eggs would be from the same clutch).

Each experiment consisted of 50 completely randomized trials. Eggs were randomized by gently shaking them in a large paper bag and blindly drawing them. Neither the presenter (P. Martin) nor the observer (myself) knew what the correct match was (or in trials 2 and 4, whether or not there was a correct match); however, the observer was aware of the rules for each experiment beforehand (i.e., that there was a 50% chance of no correct answer in

Experiments 2 and 4). Eggs were examined in natural light. I found it helpful to examine eggs in both direct sunlight and shade. Criteria used in comparing eggs included background color, spot density, spot color, spot size, surface texture (glossy *vs.* granular), and overall size and shape. Decisions were made quickly (i.e., ≤ 2 min, often within seconds). If I had difficulty deciding whether or not an egg matched another, this uncertainty was recorded.

A2.3. RESULTS AND DISCUSSION

I obtained approximately 90% correct classification in all experiments except Experiment 2, where I was only 68% correct (Table 1). In all four experiments, correct classification was higher if I excluded trials where I had expressed uncertainty (uncertainty was recorded in 10 - 24% of trials); however, classification improved markedly only in Experiment 2 (Table 1).

A2.3.1. *Implications for detecting brood parasitism.*

It apparently was easier to identify "odd" eggs from within a single clutch (Experiments 3 and 4) than it was to match such eggs to their respective sources (Experiments 1 and 2). Based on my success rate in Experiments 3 and 4, I conclude that in most cases external egg characteristics provide a reliable method for identifying parasitic coot eggs from within a normal coot clutch. Identification of parasitic eggs in host clutches is facilitated if nests are visited frequently during laying, so that parasitized nests can be recognized by laying-rate criteria (parasitic coots do not remove host eggs when laying parasitic eggs; Arnold, *pers. obs.*). Success in matching a single egg to a potential source clutch was fairly high when there were only 6 potential sources and all were known (Experiment 1), but success dropped markedly when half of the eggs had no known source (Experiment 2). An analogy to Experiment 1 would be a small wetland with a few nesting coot pairs, where one coot had parasitized another's nest but also had a nest of her own. Matching the known parasitic egg(s) to the nest of the parasitic female would be relatively easy. Experiment 2 would resemble a situation where there was an equal likelihood of a parasitic individual being another nesting female <u>or</u> a non-nesting floater with no available clutch for comparison. During 1990, I positively identified three sets of parasitic eggs as belonging to females that had just lost their clutches (see Appendix 4), but two other sets of parasitic eggs were definitely not produced by any females that previously or subsequently nested on the same wetland. In a much more extensive study of brood parasitism in American Coots, Lyon (*in press*) showed that most parasites are neighboring territorial breeders, but a few also appear to be non-nesting floaters.

A2.3.2. *Implications for renesting studies.*

Potential renests are probably easier to identify then potential parasites; most suspected renests (based on egg-matching criteria) were initiated soon after the previous nest was destroyed or abandoned, and were usually in close proximity to the previous nest (i.e., < 7 d and < 30 m, respectively; Chapter 3, Arnold *unpubl. data*). Conversely, nests suspected of being renests based on spatial and temporal proximity to a destroyed nest virtually always had similar appearing eggs; this was true of continuation nests (original nest destroyed during laying, replacement nest initiated immediately as part of the same laying sequence) and typical renests (original nest destroyed during incubation, ovary and oviduct regressed, 4 - 7 d renesting interval) (see Chapter 3, Appendix 4). Because I studied renesting by experimentally removing clutches, I had whole undamaged eggs (I saved 2 per clutch) to compare with future suspected renest clutches. I also identified renest clutches using large eggshell fragments or abandoned eggs from naturally destroyed clutches. I doubt that egg matching criteria would be as reliable if only small eggshell fragments could be salvaged from the original nest. I could often salvage an undamaged egg at destroyed nests by feeling around on the pond bottom near the base of the nest; however, such eggs had usually become stained and were less useful for comparative purposes (although size, shape, and spotting pattern were unaffected).

A2.3.3. *General comments.*

I did not assess observer-expectancy bias in these experiments (e.g., Balph and Balph 1983), but given the subjective nature of this technique, biases may be prevalent. I suspect that if I had been told I was doing Experiment 1, but was actually doing Experiment 2 (or vice versa), my initial error rate would have been quite high (I doubt that I could have been fooled for long). Such a circumstance might occur if investigators had no auxillary information available, and if they had preconceptions about the likelihood of renesting or brood parasitism in their study population. Based on my own recent observations of high parasitism and renesting among coots (see also Lyon *in press*), I suspect that many previous coot researchers (myself included) failed to detect cases of parasitism and renesting because they were not expecting them.

TABLE A2.1. Classification success [# correct/total # (% correct)] in four egg recognition experiments.

	All trials		Certain[a]		Uncertain[a]	
Expt. 1	43/50	(86)	31/34	(91)	12/16	(75)
Expt. 2	34/50	(68)	29/35	(83)	5/15	(33)
Expt. 3	47/50	(94)	42/44	(95)	5/6	(83)
Expt. 4	47/50	(94)	41/42	(98)	6/8	(75)

[a] "Certain" category represents those trials where I was reasonably confident I was correct; "uncertain" category represents trials where I had expressed reservations.

APPENDIX 3. MEASUREMENT ERROR OF EXTERNAL MORPHOLOGICAL CHARACTERS, EGG DIMENSIONS, AND AGING CRITERIA

I determined relative measurement error of several external morphological characters of American Coots and their eggs using repeated measurements and Model II Analysis of Variance (Bailey and Byrnes 1990, Lougheed *et al.* 1991). In addition, I examined the effects of such errors on relative measurement error of the first principal component (PC1) of the morphological data. PC1 is commonly used as an index of body size in studies of nutrient reserve dynamics (Alisauskas and Ankney 1987, Ankney and Afton 1988), and it was also used for that purpose in this study (Chapter 5, Appendix 5).

Thirteen morphological characters (descriptions of variables and measuring techniques are given in Section 5.2.1) were measured twice on each of 50 adult coots (26 males and 24 females; sex determined by dissection). Measurements were taken on all birds in a sample before individuals were remeasured; these remeasurements were made without knowledge of previous measurements.

Length and breadth were measured twice on each of 76 coot eggs, and volume was calculated for each set of measurements using Hoyt's (1979) equation. Unlike the morphological measures, most of these remeasurements were taken blindly (i.e., the measurer was not aware that remeasurements were being taken and would be used to assess measurement errors).

Putative age was assessed from tarsal coloration, as described by Crawford (1978), except that I recognized more variation in coloration than did Crawford (i.e., observed variation was continuous, ranging from pale green to bright yellow streaked with flame red, and hence coots did not fall neatly into 4 categories, as suggested by Crawford's scheme). In addition to Crawford's (1978) four adult age categories (1, 2, 3, and 4^+), I recognized intermediate categories based on one-third fractions (e.g., 1(2) = 1.3, 3(2) = 2.7). These fractions do not represent estimated fractional ages (coots are born into a highly seasonal environment, with most members of particular year-classes separated by < 1 month of age; Fig. 3.1), rather they represent my uncertainty at classifying individual coots to a particular age class. One hundred coots were aged twice each, once on the day of collection and again after they had been frozen for several months pending dissection. Average pre- and post-freezing age estimates did not differ (paired t-test, $t = 0.88$, $P = 0.38$), suggesting that tarsal color was unaffected by freezing.

Morphological measurements and age classes were determined by one observer (myself), but egg measurements included both inter- and intra-observer measurement errors.

Model II ANOVA (PROC NESTED; SAS Institute Inc. 1985) was used to determine percent measurement error (%ME) for each morphological character. After estimating within and among bird components of variance, I calculated %ME using the following forumula (Bailey and Byrnes 1990):

$$\%ME = (s^2_{within} / s^2_{among} + s^2_{within}) \times 100$$

I then employed principal components analysis (PCA) using the correlation matrix based on untransformed data (PROC PRINCOMP; SAS Institute Inc. 1985). I thereby obtained two independent PC1 scores for each bird, and I again used a Model II ANOVA to examine relative measurement error of these scores.

Measurement errors for external characters of American Coots were relatively low for total length, wing chord, tarsus length, middle toe length, middle claw length, and culmen length, but high for total wing length, hind toe length, bill width, and head width (Table A1.1). Relative measurement errors were lower for the entire sample than within sexes because of greater average variation among birds in the pooled sample (Table A1.1; see also Alisauskas and Ankney 1987). Among variables, %ME of the male data was highly correlated with %ME of the female data (Table A1.1: $r = 0.81$, $P < 0.01$); apparent differences of %ME between sexes were due, at least in part, to "glaring errors" made obvious only because of replication, and therefore not excludable from an analysis of measurement error (e.g., high %ME for female bill length was due to one such error).

The first principal component was little affected by measurement error (Table A1.1: 0.72 to 2.18 %ME). Nevertheless, by eliminating individual variables with high %ME from the PCA, %ME of PC1 was reduced. I deleted total wing length, hind toe length, bill width, and head width (Table A1.1) and recalculated PC1 for the different data sets. Percent ME was reduced from an average of 1.60 in the earlier analysis to an average of 1.12 with the reduced number of variables. This reduction in %ME was not offset by a loss of information on overall body size; PC1(reduced) was more highly correlated with lean dry mass than was the original PC1 (r^2 increased by 0.104 and 0.043 for males and females, respectively). Additional PC axes (i.e., the second and subsequent axes) are usually interpreted as indicators of body shape (Pimentel 1979, Rising and Somers 1989). Relative measurment error of these "shape" axes were far higher than for PC1 (Lougheed *et al.* 1991), reflecting the relatively greater measurement errors of variables important in defining these components, as well as the reduction in among-bird variation associated with these axes. PCA based on variance-covariance matrices of log-transformed data (as compared to correlation matrices of raw data) were even more obviously affected by raw variables with high relative error (Lougheed *et al.* 1991).

Length, breadth, and estimated egg volume were virtually free of measurement error (0.12, 0.59, and 0.34 %, respectively).

Percent ME for age classification was 21.2%. The 95% CI of within-bird variation ranged from -1.0 to +1.0 (data were in increments of 1/3). Only 45/100 (45%) coots were aged identically in the two trials; this increased only slightly when estimates were rounded to the nearest integer (64% consistent classification).

Based on these findings, I elected to exclude four morphological variables (total wing length, hind toe length, bill width, and head width) from future analyses of body size variation. I concluded that PC1 accurately assesses among-coot variation in body structure, and that linear measurements accurately assess among-egg variation in volume. The high %ME for age class was somewhat alarming, and I have additional reservations about this technique due to somewhat low concordance between age estimates based on tarsal coloration and age estimates based on presence or absence of the bursa of Fabricius. On the basis of these considerations, I decided to include age estimates based on the bursa of Fabricius, in addition to the more widely used tarsal coloration scheme of Crawford's (1978). For coots that had been aged twice, I used the mean age-class in analyses; this served both to reduce random measurement errors and to make age-classes more continuous.

Table A3.1. Mean, coefficient of variation, and percent measurement error of external mophological characters of American Coots.

	Males			Females			Both		
Variable:	X	CV	%ME	X	CV	%ME	X	CV	%ME
Total length	380.0	3.30	6.82	355.3	2.80	11.32	368.1	4.56	3.74
Wing length	305.5	3.62	31.89	283.1	3.48	39.69	294.8	5.21	19.06
Wing chord	204.6	3.13	3.82	188.6	3.28	4.29	196.9	5.17	1.59
Tarsus	57.35	3.60	2.54	53.14	3.30	2.97	55.33	5.15	1.25
Middle toe	77.52	3.79	2.38	72.00	3.57	2.06	74.87	5.07	1.05
Middle claw	14.80	7.73	1.99	13.19	8.59	1.82	14.03	9.90	1.31
Hind toe	25.20	6.39	19.29	23.71	5.08	21.54	24.49	6.55	16.10
Culmen	51.85	3.30	1.92	48.46	4.09	4.61	50.22	4.98	1.88
Bill length	31.63	3.56	5.14	29.20	4.38	18.14	30.46	5.60	5.73
Bill height	13.18	5.08	14.47	11.89	4.72	14.29	12.56	7.12	7.12
Bill width	10.07	15.37	18.08	8.80	16.17	35.42	9.46	17.00	15.55
Head length	68.26	2.66	18.25	63.96	2.01	10.26	66.20	4.04	5.87
Head width	23.35	3.95	24.13	21.70	2.50	15.37	22.56	4.99	10.65
PC1	(33.62)[a]		2.18	(36.17)[a]		1.91	(64.90)[a]		0.72
Age class	--	--	--	--	--	--	2.04	34.3	21.22

[a] Value in parentheses with PC1 is the percentage of total variance accounted for by PC1.

Appendix 4. Laying histories of individual American Coots with one or more renesting opportunities

	Init.	Day of nesting cycle (1 = date of first egg)																																																				
Female	Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
F-4029	136	0	0	0	0	0*	0p	0p	0	0	0	0	0	0	0*	-	-	0	0	0	0	0	0	0*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	I	I	I	--> HATCH														
F-4018	135	0	0	0	0	0	0*	0p	0p	0p	0	0	0	0	0	0*	0	0	0	0	0	0	0*	-	-	-	-	0	0	0	0*	-	0	0	0	0	0	0	0	0	-	-	-	--> NO RENEST												
F-4009	137	0	0	0*	0	0	0	0	0	0	0	0	0	0*	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	I	I	I	--> HATCH																							
F-4036	140	0	0	0	0	0	0	0	0	0	0	?	?	?*	?	?	?	-	-	0	0	0	0	0	0	0	0*	-	-	-	0	0	0	0*	-	-	-	0	0	0	0	0*	-	-	-	--> NO RENEST										
F-4037	135	0	0	0	0	0	0	0	0	0	0	0	I	I	I	I	I*	-	-	-	-	-	0	0	0	0	0	0	0	0*	-	-	-	-	0	0	0	0	0	0	0	0	I	I	I	--> HATCH										
F-4026	140	0	0	0*	0	0	0	0	0	0	0*	?	?	?	?	?	?	?	0*	-	0	0	0	0	0	0*	-	-	0	0	0	0	0	0	0	0	0	I	I	I	--> HATCH															
F-4040	140	0	0	0	0	0	0	0	0	0	0	0	0	I	I	I	I	I*	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	I	I	I	--> HATCH																
F-4019	131	0	0	0	0	0	0	0	0	0	I	I	I	I	I	I	I	I	I*	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	I	I	I	I	I*	?	?	?	?	?	?	?	?	?	-	-	-	-	0	0	0	0+2
F-4012	137	0	0	0	0	0	0*	0	0	0	0	0	0	0	0	0	0	I	I	I	I	I	?	?	?	?*	?	?	?	-	-	-	-	-	-	0	0	0	0	0	0	0	0	I	I	I	--> FATE UNKNOWN									
F-4022	138	0*	0	0	0	0	0	0	0	0	0	I*	0	0	0	0	0	0	0	0	0	0	0	0	0	I	I	I	--> HATCH																											
F-4015	135	0	0	0	0	0	0	0*	-	0	0	0	0	0	0	0*	0	0	0	0	0	0	0*	-	-	-	--> NO RENEST																													
F-4005	138	0	0	0	0	0	0	0	0	0	0	0*	-	0	S	S	0	0	0	0	0	0	0	0	I	I	I	--> HATCH																												
F-4013	134	0	0	0	0	0	0	0	0	0	0	I	I	I	I	I	I*	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	I	I	I	--> HATCH																			
F-4024	140	0	0	0	0	0	0	0	0	?	?	?*	?	?	?	0	0	0	0	S	0	0	S	0	0	0	0	0	I	I	I	--> HATCH																								
F-4039	138	0	0	0	0	0	0	0	0	0	0	I	I	I	I	I	I	I	I	I	I	I*	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	I	I	I	--> HATCH															
F-4056	141	0	0	0	0	0	0	0	0	0	0	0	I	I	I	I	I	I	I	I	I	I	I	I	I*	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	I	I	I	I	I*	-	-	-	--> NO RENEST							
F-4088	147	0	0	0*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	I	I	I	--> HATCH																																
F-4003	133	0	0	0	0	0	0	0	0	0	I*	-	-	-	-	0	0	0	0	0	0	0	0	0	0	I	I	I	--> HATCH																											
F-4041	138	0	0	0	0	0	0	0	0	0	0	I	I	I*	-	-	-	-	0	0	0	0	0	0	0	0	0	I	I	I	--> HATCH																									
F-4074	147	0	0	0*	0	0	0	0	0	0	0	0	?*	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	I	I	I	--> HATCH																					
F-4010	138	0	0	0	0	0	0	0	0	0	I	I*	-	-	-	-	0	0	0	0	0	0	0	0	0	I	I	I	--> HATCH																											
F-4001	131	0	0	0	0	0	0	0	0	0	I	I*	-	-	-	-	-	-	0	0	0	0	0	0	0	0	I	I	I	I*	-	-	-	--> NO RENEST																						
F-4007	139	0	0	0	0	0	0	0	0	0	0	I	I	I	I	I	I	I	I	I*	-	-	-	-	-	-	-	0*	-	-	-	-	0	0	0*	0	0	0*	-	-	-	--> NO RENEST														
F-4011	138	0	0	0	0	0*	?	0	0	0	0	0	0	0	0	0	0	0	0	I	I	I	--> HATCH																																	
F-4044	138	0	0	0	0*	-	-	0	0	0	0	0*	-	0	0	0	0	0	0	0	0*	-	-	-	--> NO RENEST																														
F-4083	145	0	0	0	0	0	0	0	0	0	I	I	I	I'	-	-	-	-	-	-	0	0	0	0	0	0	0	0	I	I	I	--> HATCH																								
F-4006	136	0	0	0	0	0	0*	0	0	0	0	0	0	0	0	0	0	I	I	I	--> HATCH																																			
F-4025	137	0	0	0	0	0	0*	0	0	0	0	0	0	0	0	0	0	I	I	I	--> HATCH																																			

Appendix 4. Concluded.

	Init.	Day of nesting cycle (1 = date of first egg)																																																					
Female	Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
F-4080	143	0	0	0	0	0	0*	-	-	-	0	0	0	0	0	I	I	I	I	I	I	I	I*	-	-	-	-	-	0	0	0*	0	0*	-	-	-	--> NO RENEST																			
F-4104	147	0	0	0	0	0	0	0	0	0	I	I*	-	-	-	-	-	-	0	0	0	0	0	0	0	I	I	I	--> HATCH																											
F-4043	140	0	0	0	0	0	0	0	0	0	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I*	-	-	-	-	-	-	0	0	0	0	0	0	I	I	I	--> HATCH														
F-4060	142	0	0	0	0	0	0	0*	0	0	0	0	0	0	0	0	I	I	I	--> HATCH																																				
F-4071	140	0	0	0	0	0	0	0	0	0	I	I	I	I	I	I	I	I	I	I	I	I*	-	-	-	-	-	-	0	0	0	0	0	0	I	I	I	--> HATCH																		
F-4049	140	0	0	0	0	0	0	0	0	0	I	I	I	I	I	I	I	I	I	I	I	I	?	?	?	?	?	?	?	?	0	0*	?	0	0	0	I	I	I	--> HATCH																
F-4033	137	0	0	0	0	0*	-	-	0	0	0	0	0	0	0	0	I	I	I	--> HATCH																																				
F-4084	141	0	0	0	0	0	0	0	0	0	0	0	I	I	I	I	I	I	I	I	I	?	?*	?	?	-	-	-	0	0*	-	-	-	--> NO RENEST																						
F-4133	156	0	0	0	0	0	?	?*	?	0	0	0	0	0	0	0	0	I	I	I	--> HATCH																																		
F-4035	137	0	0	0	0	0	0	0	0	0	0	0	0	I	I	I	I	I	I	I	I*	-	-	-	--> NO RENEST																															
F-4046	138	0	0	0	0	0*	-	-	-	-	0	0	0	0	0	0	0	I	I	I	--> HATCH																																		
F-4082	144	0	0	0	0	0*	-	0p	0	0	0	0	0	0	I	I	I	--> HATCH																																						
F-4051	140	0	0	0	0	0	0	0	0	0	0	0	I	I	I	I	I	I	I	I	I	I	I	I	I*	-	-	-	--> NO RENEST																											
F-4055	148	0	0*	-	0	0	0	0	0	0	0	0	0	I	I	I	--> HATCH																																							
F-4027	140	0	0	0	?*	0	0	0	0	0	0	0	I	I	I	--> HATCH																																								
F-4034	138	0	0	0	0	0	0	0	0	I	I	I	I	I	I	I	I	I	I	I	I*	-	-	-	-	-	-	0	0*	-	-	-	--> NO RENEST																							
F-4106	143	0	0	0	0	0	0	0	0	0	0	I	I	I	I	I	I	I	I	I	I	I	I	I*	-	-	-	--> NO RENEST																												
F-4132	155	0	0	0	0	?	?*	?	0	?	?*	?	-	-	-	-	-	0	0	0	0	0*	-	-	-	--> NO RENEST																														
F-4070	140	0	0	0	0	0	0	0	0	0	I	I	I	I	I	I	I	I	I	I	I	I*	-	-	-	--> NO RENEST																														
F-4094	147	0	0	0	0*	-	0	0	0	0	0	I	I	I	--> HATCH																																									
F-4105	144	0	0	0	0	0	0	0	0	0	I	I	I	I	I	I	I	I	I	I	I	I*	-	-	-	--> NO RENEST																														

Notes: F-4036's mate was killed on the nest (presumably by a Great Horned Owl) between day 11 and 16.

F-4019: +2 in right margin signifies 2 additional eggs on days 56 and 57.

0 = egg laid; p denotes parasitically laid egg; * denotes day of nest destruction; I = Incubation; - denotes renesting delay; ? = unknown.

Initiation dates are Julian date of first egg.

Appendix 5. Relationships between size of nutrient reserves and the first Principal Component (PC1) for male and female American Coots[a].

Variable	a	b ± SE	F	P	r^2	n
Females:						
Fat	29.14	1.37 ± 0.89	2.35	0.13	0.01	228
Protein	79.63	2.37 ± 0.42	31.82	0.0001	0.12	228
Ash	13.23	0.46 ± 0.09	27.41	0.0001	0.11	228
Ingesta	31.59	0.34 ± 0.91	0.14	0.71	0.00	228
Males:						
Fat	40.78	2.14 ± 1.09	3.88	0.05	0.02	211
Protein	104.36	2.67 ± 0.53	25.14	0.0001	0.11	211
Ash	17.68	0.26 ± 0.10	6.44	0.01	0.03	211
Ingesta	42.61	1.36 ± 0.93	2.15	0.14	0.01	210

[a] PC scores were obtained for each sex separately using the correlation matrix from untransformed morphological variables (see Chapter 5.2 and Appendix 3) (PROC PRINCOMP, SAS Institute Inc. 1985). Data set for this analysis includes all adult birds used in analyses in this thesis, plus additional adult birds in non-breeding, molt, post-molt, and fall migration categories (Arnold, unpubl. data; C. D. Ankney, unpubl. data). Based on these results, protein and ash were adjusted for body size in both sexes. Fat and ingesta were not adjusted for body size variation.

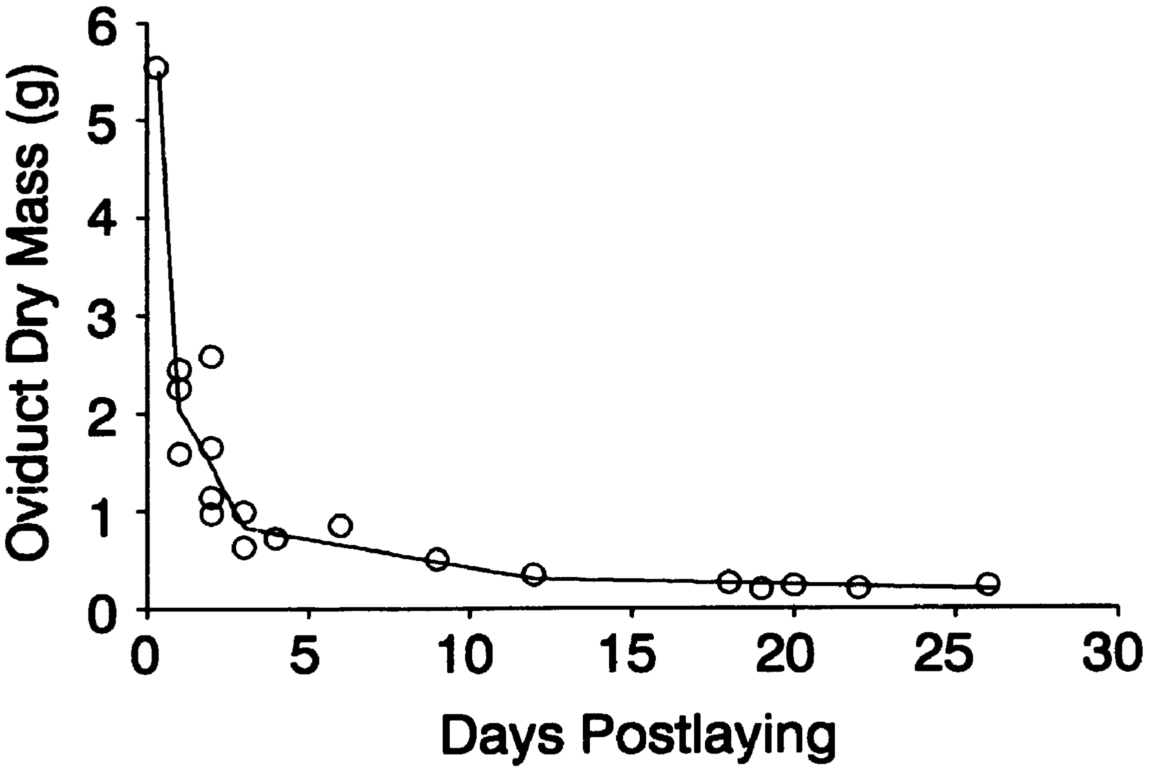


Fig. A6.1. Regression of the oviduct among postlaying American Coots. Birds were collected from nests with known laying histories. The segmented trend line was fitted by eye.

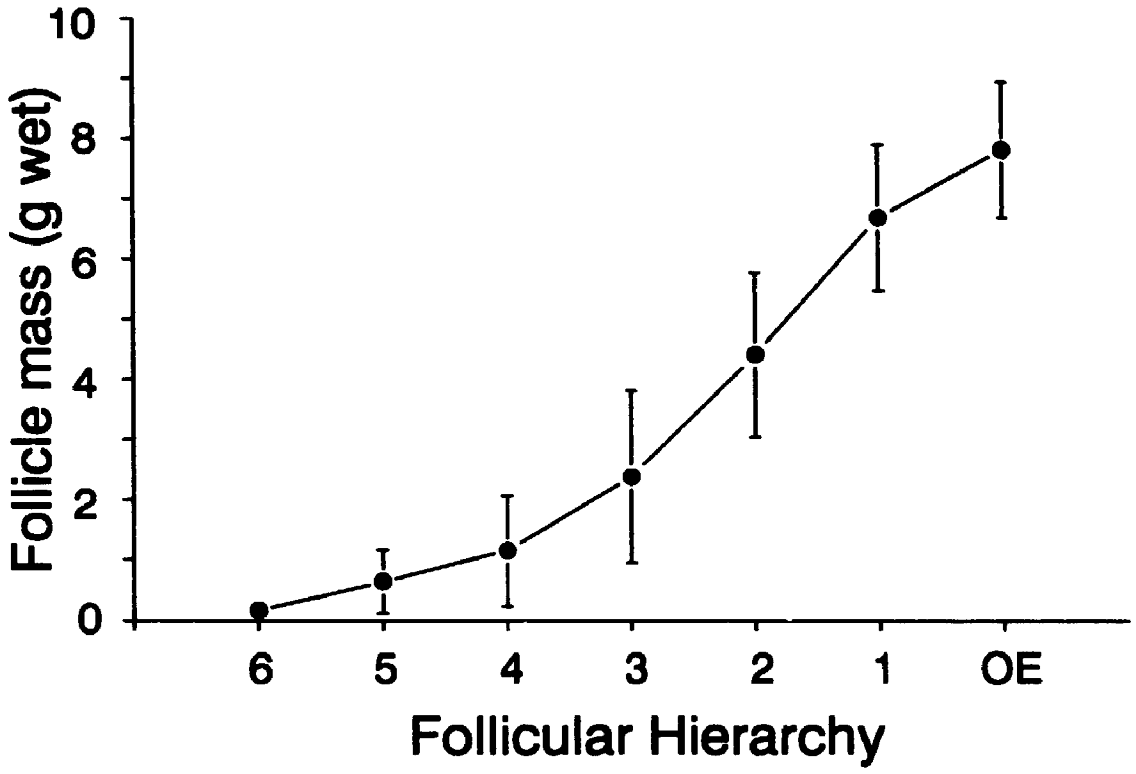


Fig. A6.2. Growth rate of developing ovarian follicles among laying American Coots. Error bars are 1 SD. OE are yolks from oviducal eggs. Sample based on 20 ovaries with full undamaged hierarchies of developing follicles. Birds exhibited substantual variation in number of developing follicles (X = 4.2, SD = 1.1, range = 3 to 6).

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