

EXAMINING POSTOVULATORY FOLLICLES OF POST-BREEDING MALLARDS:
IMPLICATIONS FOR ESTIMATES OF BREEDING PROBABILITY

by

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Breeding probability is a vital component of waterfowl recruitment, and thus greatly affects population dynamics. Despite its significance, breeding probability remains difficult to measure in most waterfowl populations. In this study, I attempted to develop and validate a new method to estimate breeding probability of free-ranging mallards (*Anas platyrhynchos*) by examining postovulatory follicles (POFs). During 2002-03, ovaries were removed from 48 mallard females (24 captive, wild-strain and 24 radio-marked, free-ranging) with known laying histories at periods ranging from 30-90 days post-laying (DPL). Examination of ovaries revealed that ≥ 1 POFs remained macroscopically identifiable in all hens (24 of 24) collected at 30-60 DPL, and for 79.2% (19 of 24) of hens collected at 61-90 DPL. Microscopic examination of cross-sectioned ovaries further demonstrated that POFs remained discernable up to 90 DPL. Blind tests using ovaries from known non-breeding hens confirmed that independent observers properly distinguished breeding from non-breeding hens 100% of the time up to 60 DPL. Ovary mass declined from 30-60 DPL, and reached a quiescent state at approximately 60 DPL. I detected no differences in ovary regression rates between captive and free-ranging females allowed to fully incubate a clutch, suggesting that captivity had no physiological impact on POF envelopment. My findings indicate that POF examination

may provide a viable method to estimate breeding probability in free-ranging mallard populations. Further investigation is needed to design a collection regime that would ensure a random, representative sample of breeding and non-breeding hens at a landscape scale. Future development and adoption of this technique could greatly enhance our understanding of mallard demographics and facilitate management decisions. My results also suggest that POF examination may be a useful method to estimate breeding probability in other waterfowl species.

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GENERAL INTRODUCTION

North American waterfowl exhibit a wide range of reproductive strategies (Johnsgard 1978, Bellrose 1980, Laurila 1988, Rohwer 1992). Reproductive performance often differs among species in relation to age and past breeding experience (Johnson et al. 1992). For example, most dabbling ducks (*Anas* spp.) are capable of breeding as yearlings, whereas diving ducks (*Aythya* spp.), sea ducks (Mergini Tribe), and geese (Anserini Tribe) typically do not breed until 2-3 years of age (Bellrose 1980). Generally, large-bodied waterfowl such as geese, sea ducks, and some diving ducks (e.g., canvasbacks; *Aythya valisineria*) survive at high rates with low annual productivity (e.g., small clutch sizes, low reneating propensity) relative to dabbling ducks. In contrast, most dabbling ducks attempt to maximize offspring production (e.g., larger clutch sizes, ability to reneat several times), while surviving at lower rates (see Rohwer 1992 for review). Although reproductive strategies differ considerably among species, the proportion of sexually mature females within a population that breed each year (hereafter “breeding probability”) is a fundamental demographic parameter for all waterfowl populations (Johnson et al. 1992)

Factors most notably influencing breeding probability in waterfowl include resource availability (Krapu et al. 1983), habitat conditions (Cowardin et al. 1985, Anderson et al. 2001), geographic location (Johnson et al. 1992), and the timing and duration of the breeding season (Lack 1954). Other determinants such as age (Johnson et al. 1992), past breeding investment (Viallefont et al. 1995), physical condition (Cowardin et al. 1985), and social behavior (Johnson et al. 1992) can also dictate breeding success.

Despite its importance to population dynamics (Johnson et al. 1992) and lifetime reproductive success (Stearns 1992), breeding probability remains difficult to measure in most waterfowl populations.

Some studies have used mark-recapture techniques to estimate breeding probability in highly philopatric species, such as lesser snow geese (*Chen caerulescens caerulescens*; Viallefont et al. 1995), black brant (*Branta bernicla nigracans*; Sedinger et al. 2001), and canvasbacks (Anderson et al. 2001). For example, Sedinger et al. (2001) used a full-likelihood modification (Kendall and Nichols 1995) of Pollock's (1982) robust design to estimate age-specific breeding probability in color-banded colonial nesting brant. Anderson et al. (2001) directly estimated breeding probability of nasal-marked female canvasbacks using a mark-resight Cormack-Jolly-Seber analysis and similar methods have been used to estimate age of first breeding in lesser snow geese (Viallefont et al. 1995).

Although detection probability can be used to index breeding probability (Lebreton et al. 1990), this method often produces confounding results (e.g., Newton 1988). For instance, this approach may not distinguish between individuals that were either: (1) breeders that departed the study area to nest elsewhere (MacInnes and Dunn 1988), (2) breeders that were present but were undetected, or (3) non-breeders (Sedinger et al. 2001). Detection probabilities can also confound estimates of breeding probability if they include individuals present that never attempted to breed (i.e., non-breeders thought to be breeders) or if early nesting attempts are undetected (i.e., nests that are abandoned or destroyed; Anderson et al. 2001). Detection probabilities are not an

effective method to estimate breeding probability of dabbling ducks. Instead, breeding probabilities for mallards (*Anas platyrhynchos*) have been estimated by radio-marking decoy-trapped hens prior to nesting. Results from these studies have led most researchers to assume that breeding probability is approximately 1.0 when spring habitat conditions are wet (Johnson et al. 1992, Rohwer 1992). More recent studies, however, suggest mallard breeding efforts may be much lower in regional populations outside the prairies.

For example, in 2001-2003, Ducks Unlimited conducted a large-scale assessment of mallard breeding ecology within the Great Lakes Region of the United States and found that approximately 84% (381 of 453) of radio-marked, decoy-trapped hens initiated a nest (J. Coluccy, unpubl. data). Similarly, in 2004, researchers documented that only 71% (24 of 34) of radio-marked, decoy-trapped females initiated a nest in California's Sacramento Valley (S. Oldenburger, unpubl. data). These data indicate that a substantial proportion of hens may forgo breeding, and this proportion varies both spatially and temporally.

Previously, researchers have radio-marked a large number of pre-breeding female mallards to assess reproductive performance (e.g., Gilmer et al. 1974, Cowardin et al. 1985, Pietz et al. 1993, Rotella et al. 1993, Paquette et al. 1997), but marking and monitoring many individuals makes these projects costly and logistically difficult. Radio-marking pre-breeding females has also been shown to adversely impact breeding behavior (e.g., Pietz et al. 1993, Rotella et al. 1993, Paquette et al. 1997), and so may not be a reliable technique to estimate breeding probability. Furthermore, decoy-trapping

methods used to capture females prior to radio-attachment may not account for a large proportion of non-breeding individuals. An alternative approach to estimate breeding probability may be to examine postovulatory follicles of unmarked females following the breeding season.

Postovulatory follicles (POFs) are portions of the ovarian follicle that remain attached to the ovary following ovulation (Davis 1942*a*). The examination of POFs has been used commonly in birds to determine whether egg laying occurred during the most recent breeding season (Davis 1942*b*, Hannon 1981) and to estimate the number of eggs laid during that period (Buss et al. 1951, Davis 1958, Payne 1965, 1973, Ankney 1974, Kennedy et. al 1989, Arnold et al. 1997, Pearson and Rohwer 1998, Curson and Mathews 2003). Although POF examination has been used for a number of bird species, the success of this technique varies considerably among taxa, study design, and laboratory methods (Kabat et al. 1948, Payne 1973, Ankney 1974, Kennedy et al. 1989, Semel and Sherman 1991, Arnold et al. 1997).

Previous research has shown that POFs remain detectable for < 30 days following ovulation in female wood ducks (*Aix sponsa*; Semel and Sherman 1991) and presumably for a similar length of time in northern pintail (*Anas acuta*), American wigeon (*A. americana*) and lesser scaup (*Aythya affinis*; Esler 1994). Alternatively, POFs have been used to accurately estimate clutch size up to 24 days post-laying (DPL) in female lesser snow geese (Ankney 1974), and these structures may persist for several months following ovulation in mallards (Lofts and Murton 1973:45, Johnson 2000:571). The length of time POFs remain recognizable also can be extended via microscopic examination of ovaries

that have been by serially cross-sectioned and stained (Payne 1966, 1973). Review of existing literature, however, indicates that this method has not been tested in mallards.

The goal of this study was to determine if POFs remain distinguishable long enough following the breeding season to estimate breeding probability in free-ranging mallards. Specifically, in **Chapter 1**, I address 2 primary objectives: (1) determine if POFs can be identified either macro- or microscopically up to 90 days following the cessation of egg-laying in captive, wild strain mallards; and (2) validate these findings on free-ranging, radio-marked hens breeding within the Central Valley of California. The development and success of this technique could greatly enhance our understanding of mallard demographics and facilitate future management decisions.

Although numerous studies have examined POFs in birds (see Semel and Sherman 1991 for review), few have investigated factors that influence POF envelopment in waterfowl (but see Esler 1994). To address this lack of information, in **Chapter 2**, I will focus on various ecological and physiological factors that could influence POF envelopment. Specific factors that I investigated include: (1) individual body condition, (2) clutch size, (3) hen age, (4) brood behavior, (5) laying groups, (6) ovary weight, and (7) the number of days post-laying at which hens were collected. My aim in **Chapter 2** is to improve our understanding of the potential factors influencing POF envelopment in mallards.

CHAPTER 1: POSTOVULATORY FOLLICLE PERSISTENCE IN POST-BREEDING MALLARD FEMALES

INTRODUCTION

BACKGROUND

Mallards are the most abundant and widely distributed ducks in North America (Bellrose 1980). They inhabit the most extensive breeding range of any North American duck and nest throughout much of the United States and Canada (Drilling et al. 2002). Many state, federal, and private agencies invest considerably in the research and management of mallards due to their socioeconomic value as a harvested species. Although the breeding ecology of mallards has been studied extensively (e.g., Pospahala et al. 1974, Batt et al. 1992, McLandress et al. 1996), little is known about a female's probability of breeding. Breeding probability (the proportion of sexually mature hens in a population that lay ≥ 1 egg during a given breeding season) is a fundamental life history trait that is vital to individual recruitment (Johnson et al. 1992), population abundance (Pospahala et al. 1974), and lifetime reproductive success (Stearns 1992). Despite its significance, mallard reproductive success has not been measured directly and breeding probability has not been reliably estimated (Drilling et al. 2002).

Currently, researchers assume 95-100% of prairie-parkland nesting mallards breed when spring habitat conditions on the breeding grounds are wet (Johnson et al. 1992), yet little empirical evidence exists to support this claim. Instead, these estimates are potentially biased high because they are derived from radio-marked, decoy-trapped hens that have already established breeding territories (i.e., territorial pair water). Non-

breeding hens are not likely to establish breeding territories, and therefore, would be excluded from these estimates.

Although mallard breeding efforts decrease when wetland conditions on the prairies are dry (Hansen and McKnight 1964, Cowardin et al. 1985, Krapu et al. 1983, Johnson and Grier 1988, Johnson et al. 1992, Krapu 2000), breeding probability estimates of 95-100% are still used in current population models (e.g., Hoekman et al. 2002). More recent research, however, suggests mallard breeding probability may be much lower in populations outside the prairies. For example, in 2001-03, researchers found that approximately 84% (381 of 453) of radio-marked, decoy-trapped mallard females initiated a nest in the Great Lakes Region of the United States (J. Coluccy, unpub. data). Similarly, in 2004, researchers documented that only 71% (24 of 34) of radio-marked, decoy-trapped hens initiated a nest in California's Sacramento Valley (S. Oldenburger, unpubl. data). These findings suggest that a much lower proportion of hens may breed than currently reported.

Due to the inherent difficulties associated with measuring breeding probability, the relative impact it has on mallard demographics remains unclear. Yet, in order to maintain viable and harvestable mallard populations, managers must understand the factors influencing the finite rate of population growth (λ). Estimates of λ can be generated by incorporating all the known vital rates (e.g., nest success, hen survival, breeding probability, duckling survival, etc.) of a particular species into a life cycle model. These models serve as a tool to determine how specific vital rates affect λ (Williams and Nichols 1990). Sensitivity analysis of λ can determine how perturbations

of a specific vital rate affect λ (Wisdom et al. 2000, Mills and Lindberg 2002). Recent sensitivity analysis of mid-continent mallards found that λ was most sensitive to changes in nest success and indicated that breeding probability had little influence on λ (Hoekman et al. 2002). These results may be somewhat misleading because breeding probability estimates are derived from decoy-trapped hens (i.e., those that had already established breeding territories) and assume little demographic stochasticity. Management efforts for mid-continent mallards, however, are primarily aimed at improving nest success through habitat acquisition and improvement (U.S. Prairie Pothole Joint Venture 1995).

Although population modeling is a valuable tool, researchers are currently unable to incorporate unbiased estimates of breeding probability into mallard models (Hoekman et al. 2002). Parameterizing these models with erroneous estimates may produce spurious results regarding which vital rates are most influential on population dynamics. This may hinder the ability to accurately monitor breeding populations and could potentially misdirect management decisions.

CALIFORNIA MALLARDS

Low breeding probability would have a significant impact on mallard productivity, particularly for those breeding in California. Approximately 265,000-600,000 mallards breed annually within California's Central Valley (Trost and Drut 2003), and extensive mallard nesting effort has been documented throughout this region for more than 85 years (Grinell et al. 1918). This population comprises 50-70% of the state's total annual mallard harvest and is an important socioeconomic resource,

especially to California waterfowl hunters. Mallard recruitment within California, however, appears to be limited by unknown factors and recent survey data indicate that breeding population (BPOP) indices have declined since 1999 (California Department of Fish and Game, unpubl. survey data 1992-2004). An inverse relationship between mallard BPOP and fall age ratio data (hatch year: after hatch year; Sheaffer and Malecki 1999), suggests that breeding probability may be one of several factors impacting population abundance.

Several hypotheses have been proposed to explain why a substantial number of these females may forgo breeding. For example, unlike most prairie-nesting ducks, California mallards breed and winter within the same geographic area. This nonmigratory nature restricts birds to acquire nutrients within the same geographic region where food resources are depleted by 3-4 million other wintering and staging waterfowl (Gilmer et al. 1982, Heitmeyer et al. 1989). Because mallards depend heavily on nutrient reserves for reproduction (Alisauskas and Ankney 1992), this depletion of available forage may lower annual productivity (Raveling 1979, Krapu 1981).

Alternatively, loss of adequate pair water or nesting cover may prevent some hens from breeding. Recent changes in agricultural practices throughout the Central Valley have resulted in a substantial loss of critical nesting habitat (Loughman et al. 2004) and significant wetland loss has occurred in this area (Gilmer et al. 1982). Intraspecific competition for limited resources (e.g., pair water, quality nesting cover) could disrupt pair bonds and lead to decreased breeding success (Johnson et al. 1992). Despite these

concerns, little research has been conducted to estimate breeding probability in California mallards.

STUDY OBJECTIVES

The goal of this study was to determine whether POFs persist long enough following the breeding season to estimate breeding probability in California mallards. Specifically, I investigated how long POFs remain following the cessation of egg laying in both captive and free-ranging hens. Mallards within the Central Valley initiate nests from late February to early June (~ 90 days; McLandress et al. 1996), which is considerably longer than prairie nesting mallards (~ 75 days from mid-April to late June; Drilling et al. 2002). Based on this nesting phenology, researchers would need to identify POFs up to approximately 75-90 days post-laying for this method to be feasible. Therefore, my specific objectives were to: (1) determine if POFs can be identified either macro- or microscopically up to 90 days after the cessation of egg laying in captive, wild strain mallards; and (2) validate these findings on a sample of free-ranging, radio-marked hens breeding within the Central Valley.

METHODS

OBJECTIVE 1. TEST WITH CAPTIVE HENS

Delta Waterfowl Research Station

Research on wild-strain, captive mallards was conducted at the Delta Waterfowl Research Station (Delta) from mid-May to early September 2002. Delta is located on the southern shore of Lake Manitoba approximately 24 km north of Portage la Prairie, Manitoba, Canada (50°11'N, 98°19'W; Fig. 1.1.). Delta's captive facilities have been used to propagate and rear waterfowl for more than 70 years. Since the early 1940's, Delta Waterfowl has also studied free-ranging waterfowl on surrounding private lands near Minnedosa, Manitoba (50°10' N, 99°47' W; Fig 1.1.).

Experimental Design

Captive Breeding Hens. – During mid-May 2002, I observed Delta's captive mallard flock to identify breeding pairs. Approximately 100-150 mature males and females were housed in an outdoor enclosure (0.5 m long x 12.2 m wide x 2.1 m high) constructed of 5.1 cm steel tubing and 2.5 cm mesh poultry netting. Once pair bonds had been established, I isolated 26 randomly selected pairs in individual breeding pens (2.1 m x 1.5 m x 0.81 m), each containing a nest box and food dish. Pairs were fitted with numbered aluminum legs bands and uniquely colored markers for individual identification (Lokemoen and Sharp 1985) and provided food and water *ad libitum*. I selected established pairs because birds allowed to choose a mate should have a higher probability of breeding than forced mates (McKinney 1992).

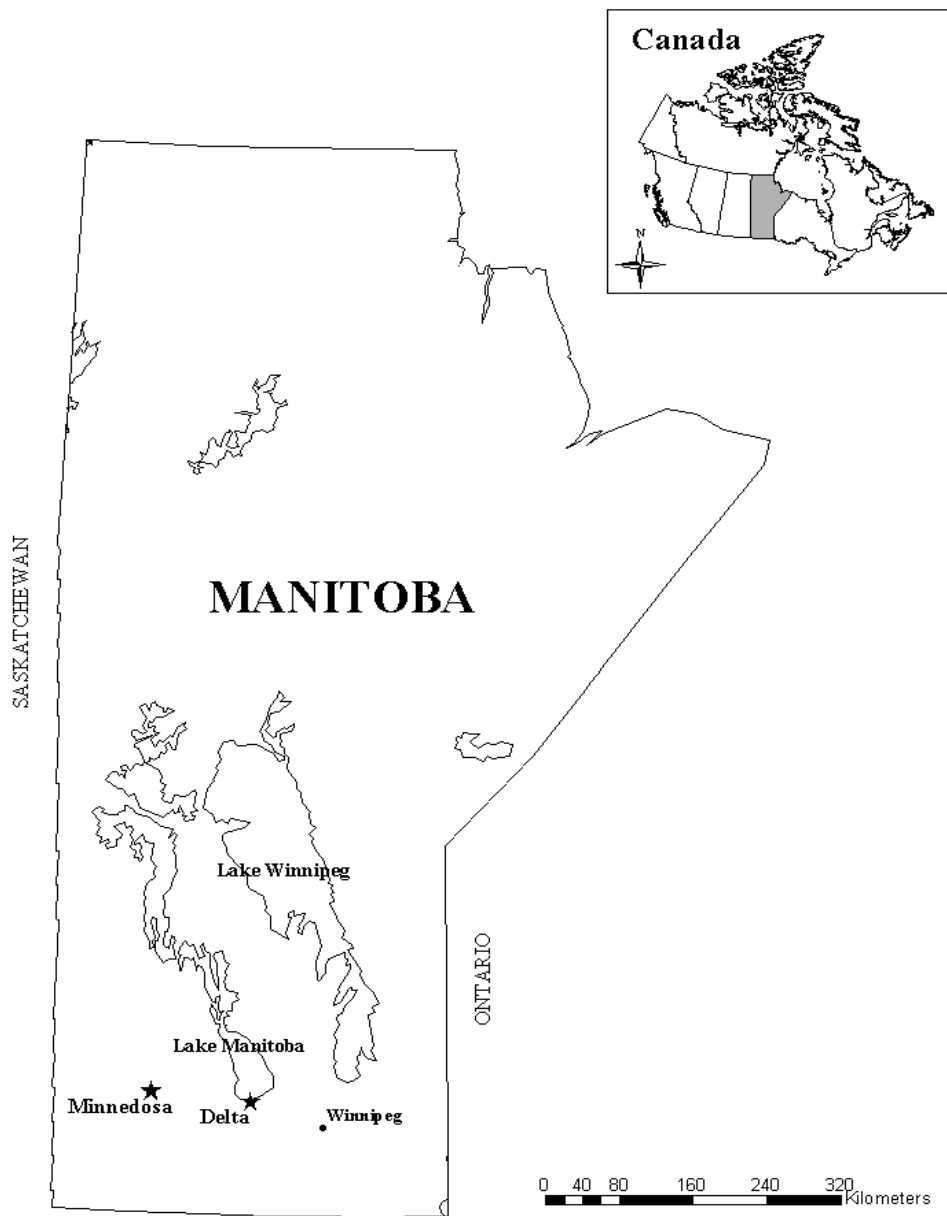


Figure 1.1. Delta Waterfowl Research Station (Delta) and Minnedosa study areas (solid stars) located in Manitoba, Canada. Research on captive mallards was conducted at Delta and wild-nesting hens were trapped from randomly selected wetlands within 20 km of Minnedosa.

Breeding pens were located outdoors to maintain ambient light and temperature conditions. Pens were constructed of 1.3-cm thick solid plywood walls and a 2.5-cm welded wire top to prevent visual and physical (but not audible) contact between breeding pairs and to increase the likelihood of successful egg laying (Batt and Prince 1979). Pens were positioned on a sloping concrete floor providing one-half swimming water and one-half dry concrete. Octagonal nest boxes and food dishes were placed on the dry concrete and fresh water was continually circulated through swimming areas. I filled nest boxes (constructed of 0.6-cm thick plywood with a 15.9 cm x 14 cm opening) with straw to provide additional nesting material. Ward and Batt (1973) describe methods for the design and construction of breeding pens and nest boxes used in this study.

Following pair isolation, I checked nest boxes 1-2 times daily (between 0700-1900 hrs) and nesting activities were recorded to determine the onset and cessation of egg laying for each hen. During daily visits, newly laid eggs were sequentially numbered, weighed (± 0.01 g) with an electronic balance, and returned immediately to the nest. I allowed nesting hens to fully incubate their clutch (ca. 23-27 days) and paired drakes were removed from pens following a week of incubation to simulate wild conditions.

Wild-Trapped Hens. – During 18 May - 2 June 2002, I also captured 11 wild hens from over-water nesting cylinders on 10 wetlands located within a 20 km radius of Minnedosa, Manitoba, Canada (50°10N, 99°47'W; Fig. 1.1.). Hens were trapped from nesting cylinders during incubation via long-handled dip nets and tunnel traps (Yerkes

1997). Following hen capture, I recorded the number of eggs laid and determined incubation stage by candling eggs (Weller 1956). Laying cessation dates were then calculated by subtracting the number of incubation days from the date of hen capture. Although incubation begins prior to the end of egg-laying (Afton and Paulus 1992), I standardized laying completion dates by assuming incubation began the day after the last egg was laid. Captured hens were also banded with U.S. Fish and Wildlife Service aluminum leg bands and color-coded tarsus bands for identification and transported to Delta's captive facilities.

To prevent injury while in captivity, hens were rendered flightless by clipping their primary feathers. Wild hens were maintained under ambient light and temperature and food and water were provided *ad libitum*. Diets for all captive birds consisted of 50% turkey starter, 48% wheat, and a 2% mixture of vitamins, grit, and ground oyster shell, used as calcium supplement for egg production. Wild-trapped hens were weighed (± 1.0 g) every 7-10 days to assess changes in body mass. Standard protocol for the care of captive birds was followed throughout (Ward and Batt 1973).

Euthanizations and Necropsies. – All hens were euthanized using an overdose of carbon dioxide in separate treatment groups at 30, 45, 60, 75 and 90 DPL with 4-6 birds per treatment (~ half captive-breeding and half wild-trapped). Following euthanization, I weighed each hen and recorded structural measurements for further analysis of individual body condition (Dufour et al. 1993, Robb 2002). I measured culmen, long tarsus, skull, and keel length (± 0.01 mm) with an electronic caliper; wing chord using a flat-edge rule

(± 1 mm); and body mass (± 1.0 g) with an electronic balance. Hens were aged as either second-year (SY) or after-second-year (ASY) females using wing feather characteristics (Krapu et al. 1979). Ovaries were surgically removed within 1 hour of euthanization, weighed (± 0.01 g), and fixed in 10% buffered formalin.

Non-breeding Hens. – During September 2002 - May 2003, an additional 9 sexually mature hens were held at Delta's captive facilities. Hens were separated from drakes to prevent breeding and subsequent egg laying. Hens were housed indoors under ambient light and temperature in spring/summer and facilities were heated during winter. Food and water were provided *ad libitum* throughout. During 30 April - 27 May, non-breeding hens were euthanized and their ovaries were removed and fixed as previously described. These ovaries were used as control samples (i.e., ovaries without POFs) in my analysis.

OBJECTIVE 2. FIELD VALIDATION

Study Area

In 2003, I conducted research to field-validate my technique on a sample of radio-marked, free-ranging mallard hens breeding within the Central Valley (CV) of California. The CV spans approximately 64 km by 644 km and comprises diverse physiognomy, biota, and climates (Heitmeyer et al. 1989). California wetlands (which exist primarily within the CV) have historically harbored one of the world's largest concentrations of wintering waterfowl, ranging from 5-8 million birds. (Heitmeyer et al. 1989). Over 95%

of historic wetlands no longer exist and only 115,000 ha remain in the CV due to anthropogenic disturbance (Gilmer et al. 1982). Most wetlands within this region have been drained or altered due to urban and agricultural development.

The CV comprises 2 lesser valleys, the Sacramento and San Joaquin Valley. The Sacramento Valley (the northern valley) is characterized by a mediterranean climate with frequent flooding during spring and winter (Heitmeyer et al. 1989). Mean annual precipitation is 50.8 cm with temperatures averaging 5 C in January and 23 C in July (Heitmeyer et al. 1989). During summer, seasonally flooded habitats dry up exposing moist soil plants and large expanses of upland nesting cover for waterfowl (McLandress et al. 1996). The combination of uplands, naturally occurring wetlands, and flooded agricultural fields, provides essential habitat for both breeding and wintering waterfowl. Heitmeyer et al. (1989:478) list a detailed description of the flora common throughout the Sacramento Valley.

Experimental Design

Site Selection. – I selected 5 search areas throughout the Sacramento Valley in which to locate mallard nests; all sites were privately-owned and located in either Colusa or Yolo County (Fig. 1.2.). Search areas consisted of 4 perennial Conservation Reserve Enhancement Program (CREP) fields (Newman, Fendt, Kalfsbeek-North, and Kalfsbeek-South) and 1 monotypic winter wheat (*Triticum aestivum*) field (Ottenwalter; Fig. 1.2.). Upland nesting habitats were dominated by Italian rye grass (*Lolium multiflorum*), canary

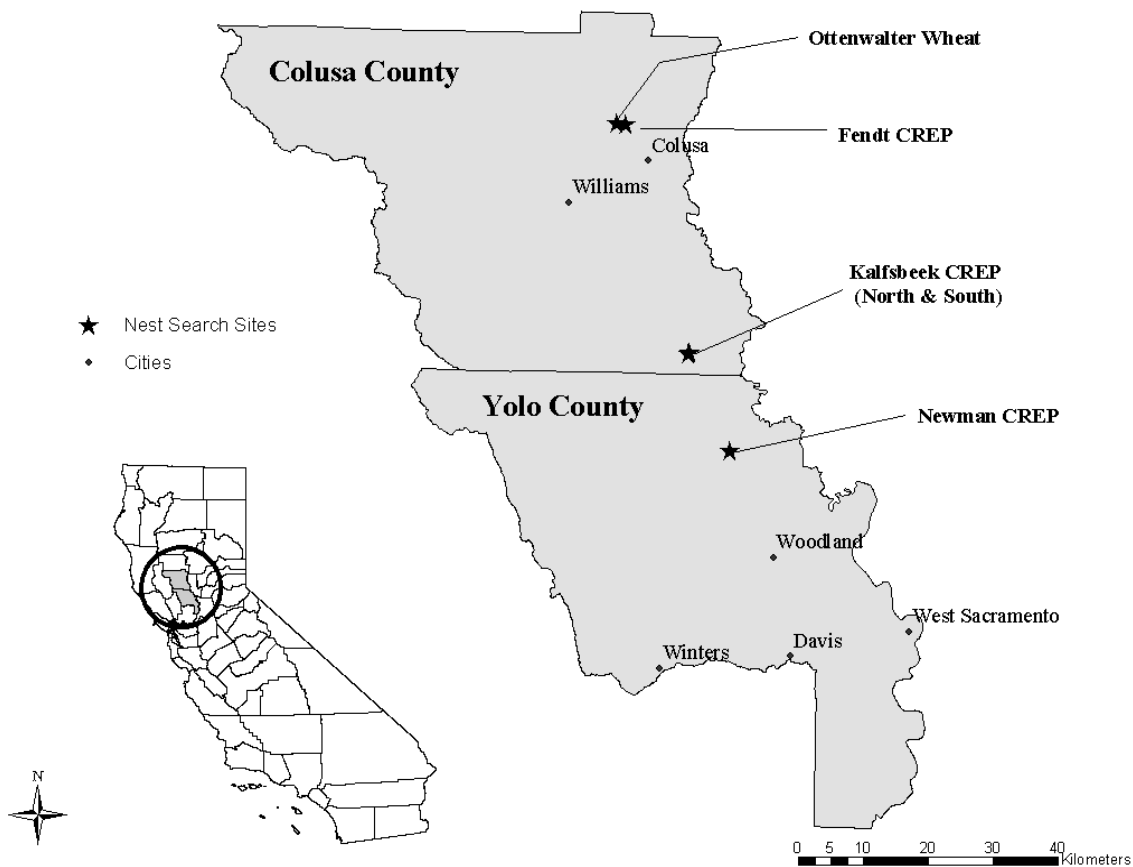


Figure 1.2. Map denoting nest search fields (solid stars) and hen capture sites in the Sacramento Valley of California, 2003.

grass (*Phalaris* spp.), rabbits-foot grass (*Polypogon monspeliensis*), wild oat (*Avena fatua*), and yellow blossom clover (*Melilotus* spp.). I selected these sites based on three *a priori* criteria: (1) ease of accessibility; (2) a long history of waterfowl research in this area; and (3) high mallard productivity has been documented throughout this region (McLandress et al. 1996, Loughman et al. 2004).

Nest Searching and Revisits. – Mallard nests were located using standard search techniques by dragging a 50 m nylon rope between two slow-moving, all-terrain vehicles (Klett et al. 1986, McLandress et al. 1996). Systematic searches were conducted from 0800 to 1400 Pacific Standard Time to maximize the probability of locating nesting females (Gloutney et al. 1993). To minimize crop damage, the Ottenwalter site was searched by hand-dragging a 25 m nylon rope between two observers. Tin cans containing stones were attached at 2 m intervals along search ropes to generate additional noise and increase the likelihood of flushing nesting hens.

Once nests were located, I counted and candled eggs to calculate laying cessation dates using previously described methods. Nest sites were recorded using a hand-held Global Positioning System (GPS) device and marked 4 m to the north with a bamboo stake to facilitate later revisits and hen capture attempts. Nests were revisited every 7-10 days to determine clutch size, embryo development, and fate (successful, depredated, or abandoned). I considered a nest successful if ≥ 1 eggs hatched and abandoned if the hen was absent from her nest, eggs were cold, and embryo development had not advanced since the last revisit (Klett et al. 1986). Nest abandonment was categorized as either

research-related or natural abandonment. Research-related abandonment resulted if a hen did not return to her nest within one day following radio attachment; whereas, natural abandonment resulted from inclement weather (e.g., extreme heat, flooding) causing premature egg death. I determined a nest to be depredated based on nest bowl and egg appearance (i.e., reduced clutch size, cached or crushed eggs) and a probable cause of predation was assigned based on shell remains.

Capture, Radio-tracking, and Collections. – Hens were nest-trapped using long-handled dip nets and modified nest traps (Weller 1957) during the last week of incubation (18-25 days). I fitted each hen with a 26-28 g external “harness-style” radio transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA) immediately following capture (Dwyer 1972). Radio-transmitters had an operational life of approximately 185 days and were equipped with a mercury switch mortality sensor. Each captured hen was also banded with a U.S. Fish and Wildlife Service leg band, weighed (± 10 g) using a Pesola spring scale, and aged as SY or ASY.

Radio-marked hens were located 2-3 times weekly with a 3-element hand-held yagi antenna to monitor post-breeding movements and re-nesting attempts. I assumed that hens left the study area if they could not be located from the ground for > 1 week. Aerial searches using aircraft (Cessna 185) equipped with antennas and a scanning receiver were conducted to locate hens that dispersed outside the immediate study area (Gilmer et al. 1981). Aerial searches ($n = 4$) were flown exclusively throughout the Sacramento Valley.

I later collected a sample of radio-marked hens at periods ranging from 34-90 DPL (similar to captive hens euthanized in 2002). Hens were located via triangulation, approached, and collected using a 12-gauge shotgun. Carcasses were recovered and GPS coordinates were recorded at each collection site. I also recorded body mass and structural measurements of collected hens as previously described. Ovaries were removed, fixed, and transported to Southern Illinois University Carbondale (SIUC) laboratory facilities for further examination. All methods were approved by the SIUC Institutional Animal Care and Use Committee (Protocol #02-003) and proper state, federal, and provincial authorities.

OVARY EXAMINATION

Macroscopic Assessment

Ovaries were examined under a 6.4-16X dissecting microscope (hereafter “macroscopically”) with no prior knowledge of laying histories to identify the presence or absence of POFs. I identified obvious POFs by their flattened/elongated shape and open stigma indicating the site of ovulation (Davis 1942*a*), but most POFs were identified as yellowish colored follicles having an occluded stigma characteristic of the terminal involution (Lewin 1963, Payne 1966, Scott and Ankney 1983, Pearson and Rohwer 1998, Curson and Mathews 2003). The number of POFs identified was recorded for each hen.

Two independent observers (Lindstrom and Eichholz) performed blind tests (no knowledge of laying histories) using a sample of ovaries collected from both breeding

and non-breeding hens. Thirty-three (24 free-ranging breeders and 9 non-breeders) ovaries were placed in jars each containing 50 ml of formalin. Independent examinations were then made and observers assigned the laying status of each ovary as: Breeder or Non-breeder. This technique allowed me to assess how accurately experienced, independent observers could distinguish breeding from non-breeding females based on POFs.

Additional blind tests were administered to assess how accurately novice individuals without extensive training could distinguish between breeding and non-breeding hens based on POFs. Observers were given a brief 1.5 hour training session on how to properly distinguish POFs. Thirty (21 radio-marked breeding hens, 9 captive non-breeding) ovaries were placed in identical, anonymously coded jars each containing 50 ml of formalin. Three ovaries used in the first blind test were excluded from this analysis because they had already been cross-sectioned (see below). Independent macroscopic inspections were then made by 2 SIUC Cooperative Wildlife Research Laboratory students (Daniel Storm and Michael Sertle) and the laying status for each ovary was recorded.

Microscopic Assessment

Following macroscopic examination, 46 of 57 ovaries (24 captive, 13 free-ranging, and 9 nonbreeding hens) were embedded in paraffin and serially-crossed sectioned at 8 μ (Payne 1966,1973). I did not cross-section all ovaries because POFs were macroscopically identifiable in most cases (see Results). I modified sectioning

procedures by mounting every 5th and 3rd section on slides for hens collected at 30-60 and 61-90 DPL, respectively. Excess paraffin was removed from slides by warming them in a 40 C oven for approximately 10 minutes and placing them in a series of vats containing HistoClear, ethyl alcohol (100% and 95%), and water. Tissues were stained (Harris' hemotoxylin), counter-stained (Eosin Y), covered, and examined under a compound microscope (hereafter "microscopically") at 20-80X magnification (Payne 1973). Microscopic POFs were distinguished from unovulated follicles following characteristics described by Payne (1966) and Erpino (1969) .

STATISTICAL ANALYSIS

Maintaining hens in captivity may have adversely affected laying behaviors; therefore, I used a one-way analysis of variance (ANOVA; PROC GLM) to compare mean clutch size among laying groups (captive breeding, wild-trapped, free-ranging). I also tested for age-specific differences (SY vs. ASY) in mean clutch size using similar methods. Individual means were adjusted with a least square means (LS Means) procedure and multiple pair-wise comparisons were made *post hoc* using Tukey's honestly significant difference (HSD) test (Sokal and Rohlf 2000).

The proportion of females with ≥ 1 macroscopic POFs was compared among laying groups using chi-squared tests. Linear regression models (PROC GLM) were also used to test for associations between apparent clutch size and macroscopic POF counts. All analyses were performed using SAS version 8.0 software (SAS Institute 1999) and considered statistically significant at $P \leq 0.05$

RESULTS

REPRODUCTIVE EFFORT

Delta Captive Breeding Hens

Nest Initiation and Clutch Size. – Twenty-six mallard pairs were individually isolated in breeding pens on 23 May 2002. Of these, 15 females laid complete clutches. Two nesting hens were censored from the analysis due to aberrant laying behaviors; one hen continued to lay eggs after an initial clutch was completed and another laid an abnormally large clutch of 28 eggs. Thus, data presented hereafter were collected from 13 (7 ASY and 6 SY) captive breeding hens.

Captive breeding hens (CBHs) generally formed a nest bowl approximately 2 days prior to egg laying and the onset of laying occurred 4 days following isolation. The central span (range from the 10 to 90 percentiles) of nest initiations was 14 days (27 May to 9 June; Table 1.1.). Mean and median nest initiation dates were 31 and 28 May, respectively, with a majority of hens (53.8%; 7 of 13) initiating nests on 27 or 28 May (Table 1.1.). Median and mean dates of laying cessation were 8 and 10 June, respectively (range 4 to 25 June; Table 1.1.).

During isolation, CBHs laid a total of 116 eggs with a mean clutch size of 8.92 eggs (± 0.57 SE, range 6-14; Table 1.1.). Mean fresh egg weight was 52.11 g (± 0.46 SE, $n = 116$) and did not differ between ASY and SY hens ($P > 0.05$). On average, CBHs laid 0.82 (± 0.57 SE) eggs per day (Table 1.1.). I detected no differences ($P > 0.05$) in clutch size between ASY ($\bar{x} = 8.42 \pm 0.78$ SE, $n = 8$) and SY ($\bar{x} = 9.5 \pm 0.85$ SE, $n = 6$) hens.

Table 1.1. Reproductive parameters recorded for 13 wild-strain, captive breeding hen (CBH) mallards maintained at the Delta Waterfowl Research Station, near Portage la Prairie, Manitoba, Canada, April-September 2002.

Hen	Age ^a	Clutch Size	Initiation Date	Completion Date	Laying Rate ^b	Incubation Days	Nest Fate ^c	Euthanization Date	DPL ^d
3808	SY	9	6/09/02	6/18/02	0.90	27	SH	7/18/02	30
3812	SY	14	6/09/02	6/25/02	0.82	26	NV	7/25/02	30
3801	SY	7	6/08/02	6/16/02	0.78	23	NV	7/31/02	45
3811	SY	10	6/02/02	6/12/02	0.91	26	SH	7/27/02	45
3807	SY	7	5/31/02	6/09/02	0.70	23	SH	8/08/02	60
3184	ASY	7	5/31/02	6/10/02	0.64	26	AB	8/09/02	60
3173	ASY	8	5/28/02	6/06/02	0.80	24	SH	8/05/02	60
3593	ASY	10	5/27/02	6/08/02	0.77	27	NV	8/22/02	75
3380	ASY	10	5/28/02	6/07/02	0.91	23	SH	8/21/02	75
3387	ASY	10	5/28/02	6/07/02	0.91	23	SH	8/21/02	75
3392	ASY	9	5/27/02	6/04/02	1.00	24	SH	9/02/02	90
2553	ASY	6	5/28/02	6/06/02	0.60	0	AB	9/04/02	90
3197	ASY	9	5/27/02	6/04/02	1.00	23	AH	9/02/02	90
(\pm SE)	--	8.92 (0.57)	5/31/02	6/10/02	0.82 (0.04)	22.7 (1.9)	--	--	--

^aSY = second-year old female, ASY = after-second-year old female.

^bCalculated as total clutch size/total number of days to complete a clutch.

^cAB = hen abandoned nest, NV = hen sitting on non-viable eggs (dead or infertile) and was removed from nest, SH = hen successfully hatched ≥ 1 egg from clutch.

^dDPL = Number of days post-laying at which hens were euthanized.

Incubation Behavior and Nest Fate. – Eight of 13 (61.5%) CBHs hatched their clutch, while the remaining 5 (38.5%) females were unsuccessful (Table 1.1.). Of the 5 unsuccessful nesters, two hens abandoned their nest after laying a complete clutch; one deserted her nest only one day following the completion of egg laying, and one abandoned an infertile clutch after approximately 26 days of incubation. Three other unsuccessful hens were removed from their nests because they were incubating non-viable (dead or infertile) eggs (Table 1.1.). Incubation periods (number of days between the completion of egg laying and nest termination) averaged 22.7 days (± 1.94 SE, range 0-27; Table 1.1.) and did not differ ($P > 0.05$) between successful ($\bar{x} = 24.1 \pm 0.59$ SE, $n = 8$) and unsuccessful hens ($\bar{x} = 20.4 \pm 5.14$ SE, $n = 5$).

Delta Wild-Trapped Hens

Trapping Success and Nesting Phenology. – From 18 May - 2 June, I trapped 11 wild hens (WTHs) from over-water nesting cylinders near Minnedosa, Manitoba. Five (45.5%) females were captured using tunnel traps and the remaining 6 (54.5%) were captured on foot or by canoe using long-handled dip nets. Generally, WTHs were captured at mid-incubation ($\bar{x} = 16.6 \pm 1.9$ SE), but were also removed opportunistically from their nests during early and late incubation periods (range 7 to 26 days; Table 1.2.). Nest initiations ranged from 21 April to 17 May (27 days) with a central span extending 16 days. Median and mean nest initiation dates were 19 and 20 May, respectively. Wild-trapped hens laid an average of 9.45 (± 0.68 SE) eggs and the mean date of laying cessation occurred on 9 May (range 1 to 22 May; Table 1.2.).

Table 1.2. Reproductive parameters of 11 wild-trapped hen (WTH) mallards captured from over-water nesting cylinders near Minnedosa, Manitoba, Canada, May-June 2002.

Hen	Clutch Size	Capture Date	Incubation Days ^a	Laying Completion ^b
013	10	5/18/02	7	5/11/02
014	9	5/18/02	17	5/01/02
015	10	5/20/02	12	5/08/02
016	11	5/20/02	19	5/01/02
017	9	5/20/02	19	5/01/02
018	12	5/30/02	20	5/10/02
019	11	5/30/02	9	5/21/02
020	12	5/31/02	22	5/09/02
021	6	5/31/02	9	5/22/02
022	5	6/01/02	23	5/09/02
023	9	6/02/02	26	5/07/02
\bar{x} (\pm SE)	9.45 (0.68)	--	16.6 (1.9)	5/09/02

^anumber of incubation days as calculated by candling eggs (Weller 1957).

^bestimated by subtracting the number of days incubation from the date of capture.

Acclimation to Captivity. – Wild-trapped hens were maintained in captivity for an average of 43.4 days (± 5.6 SE, range 21-71) prior to euthanization. During this time, hen body mass fluctuated slightly, but remained relatively stable overall (range 836-1,043 g; Fig. 1.3.). Most females (6 of 11; 54.5%) gained weight during isolation and mean body mass at the time of capture ($\bar{x} = 910 \pm 18.5$ g SE) did not differ ($P > 0.05$) from those recorded following euthanization ($\bar{x} = 905.0 \pm 15.7$ g SE; Table 1.3.). On average, hen mass fluctuated only slightly ($\bar{x} = - 5.2 \pm 20.8$ g) between the time of capture and euthanization (Table 1.3.). Although WTHs began feeding on provided diets within 24-36 h following isolation, fluctuations in body mass appeared more variable during the first two weeks in captivity and later stabilized as hens acclimated to captive conditions (Fig. 1.3.).

California Free-Ranging Hens

Nest Searching, Phenology, and Success. – During 1 April - 24 June, I conducted systematic nest searches on 136 ha throughout the Sacramento Valley. A total of 140 nests were found, with mallards comprising the vast majority (96%; 135 of 140); gadwall (*Anas strepera*; $n = 2$) and cinnamon teal (*A. cyanoptera*; $n = 3$) made up the remaining 5 nests (Table 1.4.). Median and mean nest initiations occurred on 3 and 5 May (range 16 March - 4 June), respectively. Mallard nest success was highly variable among study sites, and was the highest at the Kalfsbeek (North) site (72.96%). Mayfield nest success estimates averaged 64.06% across all study sites combined (Table 1.4.).

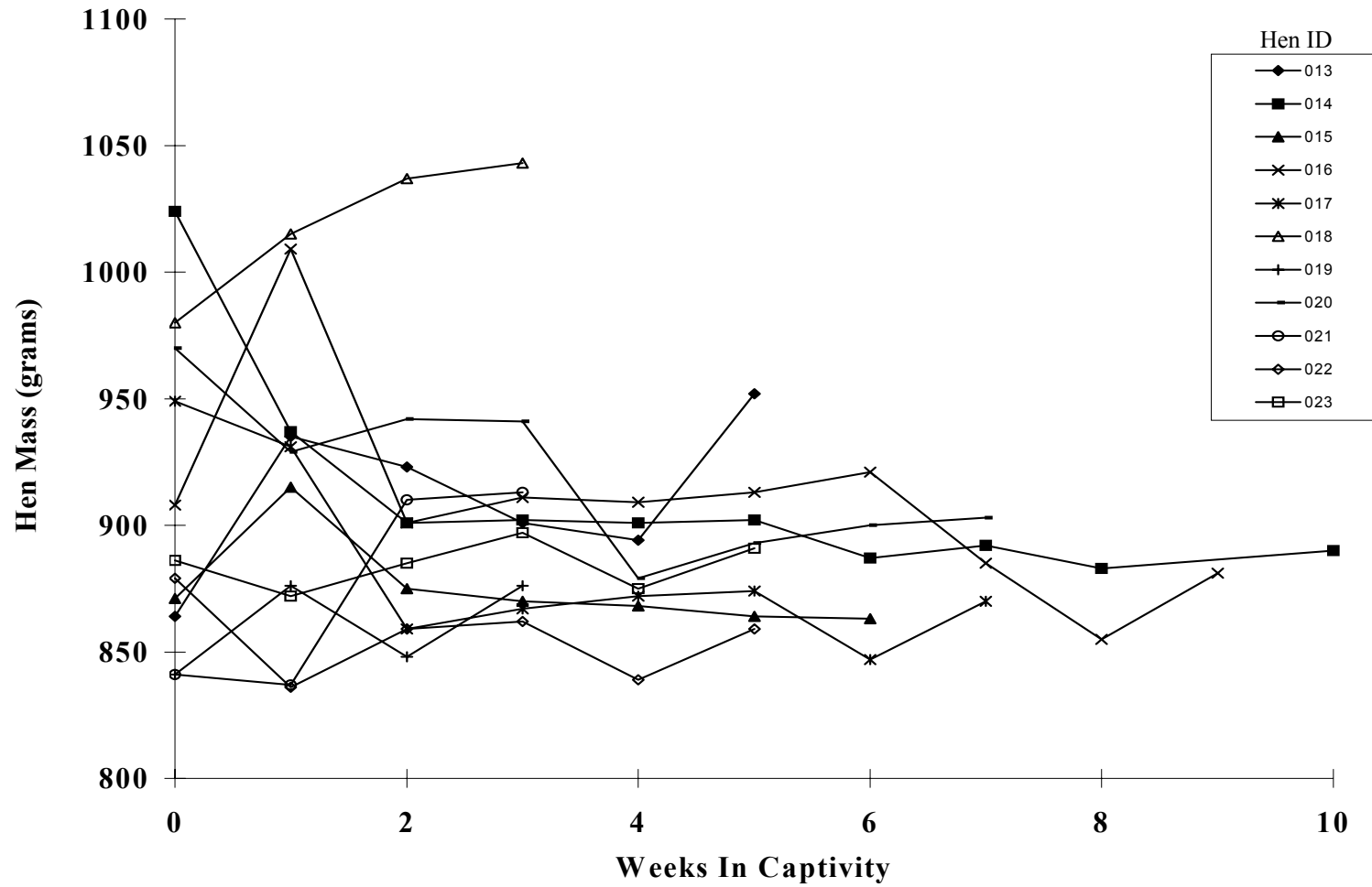


Figure 1.3. Temporal trends in body mass for 11 wild-trapped hen mallards held in captivity at the Delta Waterfowl Research Station, Manitoba, Canada, May-July 2002. Individual hens denoted in legend

Table 1.3. Changes in body mass between the time of capture and euthanization for 11 wild-trapped hen (WTH) mallards maintained at the Delta Waterfowl Research Station in Manitoba, Canada, May-July 2002.

Hen	Days in Captivity	Capture Date	Collection Mass (g)	Euthanization Date	Euthanization Mass (g)	Mass Change
013	38	5/18/02	864	6/25/02	952	88
014	73	5/18/02	1,024	7/30/02	890	-134
015	48	5/20/02	871	7/7/02	877	6
016	71	5/20/02	908	7/30/02	881	-27
017	56	5/20/02	949	7/15/02	870	-79
018	25	5/30/02	980	6/24/02	1,043	63
019	21	5/30/02	841	6/20/02	876	35
020	53	5/31/02	970	7/23/02	903	-67
021	21	5/31/02	841	6/21/02	913	72
022	37	6/01/02	879	7/08/02	859	-20
023	34	6/02/02	886	7/06/02	891	5
$\bar{x}(\pm \text{SE})$	43.4 (5.6)	--	910.2 (18.5)	--	905.0 (15.7)	- 5.2 (20.8)

Table 1.4. Search effort, number of nests found, and mallard nest success at each study site in Colusa and Yolo Counties, California, April-July 2003.

Study Site	Ha Searched	Total Nests	Mallard Nests (%) ^a	Other Nests	Hens Radio-Marked	Nest Success (%) ^b
Ottenwalter	24	36	36 (100)	--	25	71.23
Fendt	28	77	72 (94)	5	11	68.51
Kalfsbeek (North)	19	5	5 (100)	--	1	72.96
Kalfsbeek (South)	5	6	6 (100)	--	1	43.89
Newman	59	16	16 (100)	--	4	63.72
TOTALS	136	140	135 (96)	5	42	64.06

^atotal number of mallard nests found (proportion of total nests found)

^bcalculated using Mayfield nest success estimates (Klett et al. 1986)

Trapping Success, Radio-Attachment, and Hen Fate. – Between 20 April - 2 June, 42 nesting hens were captured and equipped with radio-transmitters (Table 1.4.). Twenty-seven hens (64.3%) were caught with nets and the remaining 15 (35.7%) were captured using modified nest traps. Nest traps were highly effective, with 15 of 18 (83.3%) successfully capturing females, although 3 hens abandoned their nest presumably due to human disturbance. Capture attempts using nets proved much more difficult and ineffective. Of the 42 hens captured, 25 (59.5%) were radio-marked at the Ottenwalter site (Table 1.4.; Appendix A.). Dense wheat growth at this site improved hen capture success compared to the other more sparsely vegetated CREP sites. Total handling time (time of capture to time of release) of hens during radio-attachment averaged 21.69 (\pm 0.65 SE, range 16-38) minutes.

Apparent nest success of radio-marked hens was exceptionally high, with 33 of 42 (78.6 %) successfully hatching and only 5 (11.9 %) nests were depredated (1 nest at Fendt and 4 nests at Ottenwalter). Examination of depredated nests indicated that all predation was due to mammalian predators; 3 nests presumably by raccoon (*Procyon lotor*) and 2 nests by striped skunk (*Mephitis mephitis*). Four (11.9%) females abandoned their nests following radio attachment; 2 hens abandoned nests due to investigator activity and 2 hens deserted their nests due to inclement weather (i.e., flooding or extreme heat). Hatching success for radio-marked hens was 0.60 (\pm 0.08 SE; 239 of 397 eggs; Appendix A.). Four of 42 (9.5 %) hens died prior to collection attempts. Post-mortem examination revealed mammalian predators killed 3 hens and 1 (Hen 172.571) was presumably killed by disease or adverse effects caused by radio-wear.

I was able to salvage the intact ovary from Hen 172.571 prior to carcass decomposition at 34 DPL (Table 1.5.), but the other 3 carcasses were too decomposed or consumed to recover any ovaries.

From 14 June - 16 July, I collected 23 of the 38 (60.5%) remaining radio-marked free-ranging hens (FRHs) at times ranging from 42-90 days post-laying (Table 1.5.). Hen 172.890 was also shot, but I was unable to retrieve her carcass because the radio transmitter failed (Table 1.5.). One unmarked hen sitting on non-viable eggs was also collected from her nest site at approximately 45 DPL (Table 1.5.). Hens (excluding those collected from their nest sites) were collected from a variety of habitat types at a mean distance of 4,445 (\pm 612 SE, range 408 - 12,567) meters from their original radio-attachment site (Table 1.5.). I was unable to collect the remaining 15 radio-marked hens because they had either: (1) inhabited federal refuge or private property that did not permit collections; or (2) dispersed outside the study area making collections impossible. To date, none of the 15 hens presumed to be alive at the conclusion of this study have been reported by band returns.

POF EXAMINATION

Macroscopic Assessment

During 2002-03, I collected and examined ovaries from 48 post-breeding (13 CBH, 11 WTH, 24 FRH) mallards. Mean apparent clutch size (adjusted for LS Means) did not differ ($F_{2,45} = 0.35$, $P = 0.71$) among captive ($\bar{x} = 8.92 \pm 0.55$ SE, $n = 13$), wild-trapped ($\bar{x} = 9.45 \pm 0.59$ SE, $n = 11$) or free-ranging ($\bar{x} = 9.45 \pm 0.40$ SE, $n = 24$) hens.

Table 1.5. Female mallards collected at 34-90 days post-laying from various habitat types located throughout Colusa and Yolo Counties, California, 2003.

Hen	Collection Date	Days Post-laying	Distance (m) ^a	Collection Site ^b
172.571 ^c	5/02/2003	34	1,644	SW
172.851	6/20/2003	42	3,784	FR
172.689	6/19/2003	44	871	ID
172.631	6/19/2003	45	2,224	FR
172.280 ^d	6/23/2003	45	--	NS
No radio ^e	6/18/2003	45	--	NS
172.808	7/03/2003	51	12,567	FR
172.910	6/27/2003	57	4,509	FR
172.239	6/29/2003	58	3,703	FR
172.613 ^d	6/14/2003	58	--	NS
172.890 ^f	6/30/2003	59	5,818	FR
172.472	7/01/2003	61	3,646	FR
172.413	7/01/2003	63	3,933	FR
172.710	7/05/2003	64	3,503	SW
172.902	6/30/2003	65	2,895	SW
172.423	7/01/2003	65	2,309	FR
172.771	7/02/2003	70	408	FR

Table 1.5. Continued.

Hen	Collection Date	Days Post-laying	Distance (m) ^a	Collection Site ^b
172.841	7/16/2003	72	796	FR
172.092	7/13/2003	72	9,207	FR
172.363	7/04/2003	75	5,924	SW
172.621	7/05/2003	75	5,981	SW
172.017	7/07/2003	82	5,428	SW
172.640	7/03/2003	83	4,887	SW
172.720	7/08/2003	87	7,029	FR
172.253	6/26/2003	90	6,686	SW
\bar{x} (\pm SE)	–	–	4,445 (612)	--

^aStraight line distance (m) calculated between the initial nest/radio-attachment and collection sites.

^bHabitat type where hens were collected: FR = flooded rice field, SW = seasonal or temporary wetland, ID = irrigation ditch, NS = nest site.

^cIntact ovary was removed from hen following mortality; others collected via a 12-gauge shotgun.

^dHens 172.280 and 172.613 successfully hatched a brood, later experienced total brood loss, and returned to their original nest to sit on non-viable eggs from their previous clutch.

^eNon-radio-marked hen collected from nest site.

^fUnable to retrieve hen carcass because radio transmitter failed after being shot.

Macroscopic examination revealed ≥ 1 POFs remained identifiable in 43 of 48 (89.6%) ovaries collected from 30-90 DPL (Table 1.6., Fig. 1.4.). POFs (≥ 1) were conspicuous in all CBHs (13 of 13) and for the vast majority of WTHs (90.9%; 10 of 11) and FRHs (83.3%; 20 of 24). The proportion of females with ≥ 1 distinguishable POFs did not significantly differ among groups ($df = 2$, $\chi^2 = 2.54$, $P = 0.64$; Table 1.6). Macroscopic counts also demonstrated that ≥ 1 POFs remained discernable in all females (24 of 24) collected between 30-60 DPL, and in 19 of 24 (79.2%) hens collected between 61-90 DPL (Appendix B.). The 5 of 48 (10.4%) hens that did not retain distinguishable POFs were collected at 61, 65, 70, 71, and 75 DPL (Appendix B.).

Blind Test Comparisons

Blind tests showed that both independent observers (Lindstrom and Eichholz) correctly assigned breeding status for all breeding females (10 of 10) collected at ≤ 60 DPL. More importantly, each observer correctly identified all non-breeding ovaries (9 of 9) based on the absence of POFs. Observers misidentified 4 of 24 (16.7%; both observers misidentified the same hens) ovaries from breeding hens as non-breeders due to inconspicuous POFs, albeit all of these were collected at periods > 60 DPL. Ovarian follicles regressed rapidly at periods > 60 DPL, making it difficult to distinguish breeding status for some hens collected at later post-laying periods (Fig. 1.5.).

Table 1.6. Percentage of mallard females ($n = 48$) with macroscopically identifiable postovulatory follicles collected at 30-90 days post-laying during 2002-03. Numbers in parentheses denote total number of females collected per treatment at 30-60 and 61-90 DPL.

Laying Groups	<u>Days Post-laying</u>		Total (n)	% ^a
	30-60	61-90		
Captive Breeding Hens (CBH)	7 (7)	6 (6)	13 (13)	100.0
Wild-trapped Hens (WTH)	7 (7)	3 (4)	10 (11)	90.9
Free-Ranging Hens (FRH)	10 (10)	10 (14)	20 (24)	83.3
TOTALS	24 (24)	19 (24)	43 (48)	89.6

^aPercentage of females with ≥ 1 distinguishable POFs did not significantly differ among laying groups ($df = 2$, $\chi^2 = 2.54$, $P = 0.64$).

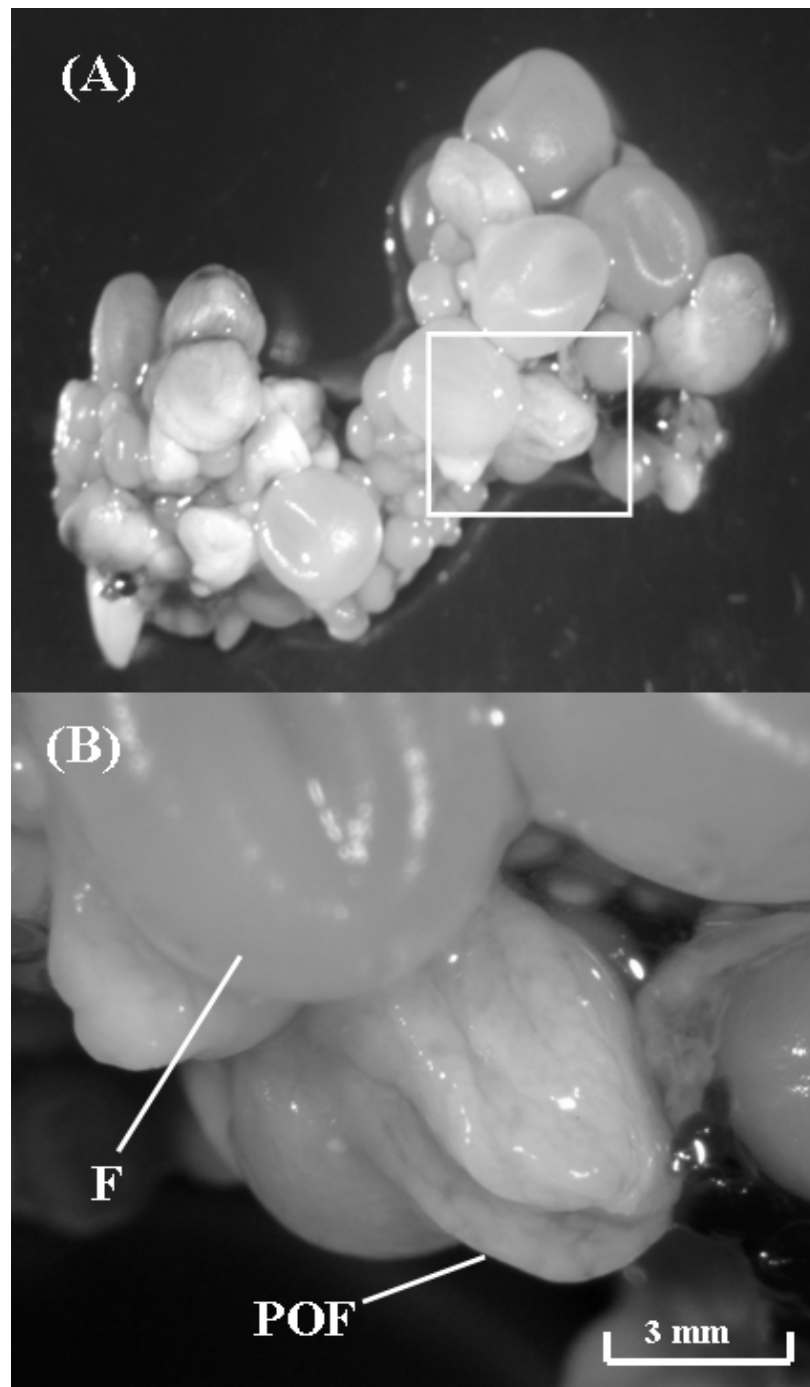


Figure 1.4. (A) Mallard ovary collected at 34 days post-laying viewed under a dissecting microscope. (B) Inset depicts the morphological differences between a postovulatory follicle (POF) and a regressing, unovulated follicle (F). Note the flattened, elliptical shape of the POF and the partially occluded stigma indicating the site of ovulation.

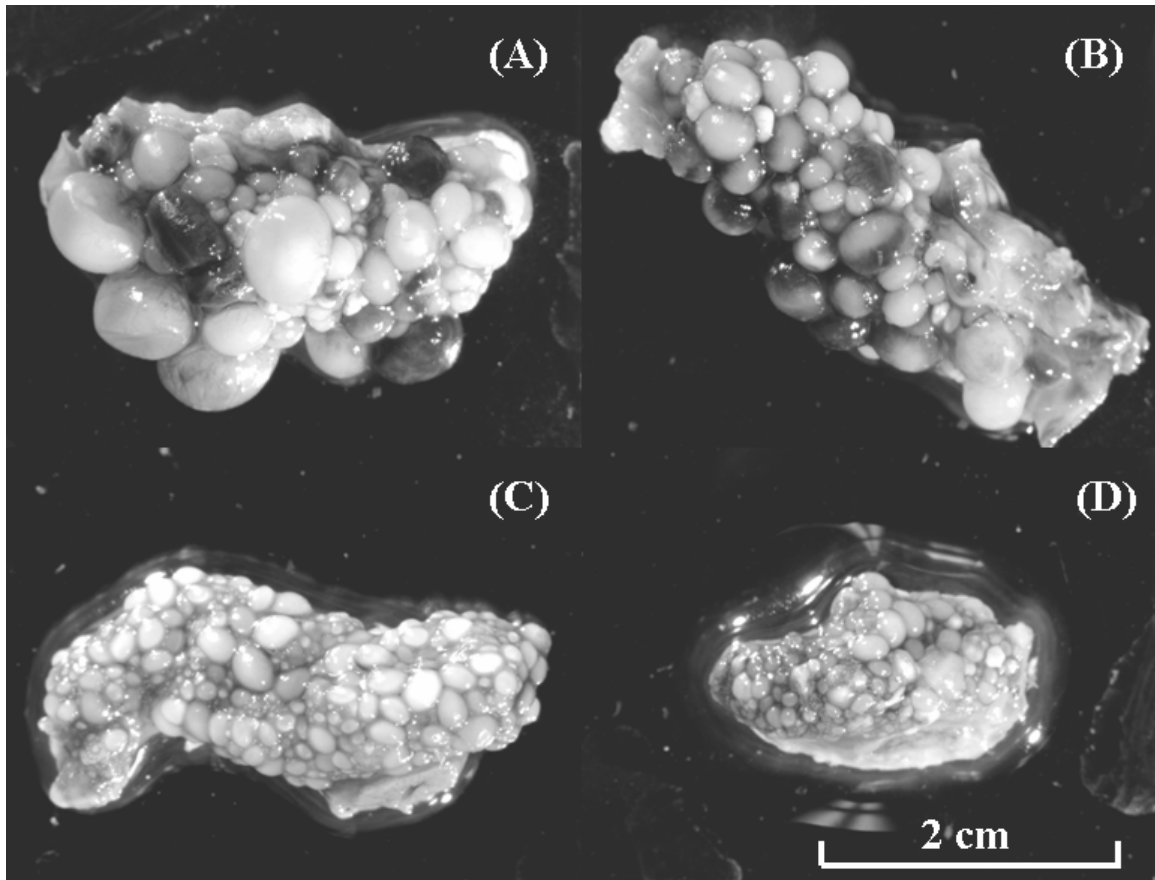


Figure 1.5. Temporal regression of mallard ovaries viewed under a dissecting microscope at (A) 45, (B) 60, (C) 75, and (D) 90 days following the cessation of egg laying.

Blind tests performed by novice observers (D. Storm and M. Sertle) further demonstrated that individuals with minimal training could correctly distinguish breeding status in most cases using POF examination. Sertle correctly assigned breeding status for all 30 (21 breeding and 9 non-breeding) ovaries during macroscopic examination. Storm correctly assigned breeding status to 26 of 30 (86.7%) ovaries, with 2 breeding hens (collected at 63 and 75 DPL) misidentified as non-breeders, and 2 non-breeders misidentified as breeders.

Microscopic Assessment

Microscopic examination increased the ability to identify POFs for a greater period of time. POFs were microscopically identifiable in all 5 ovaries lacking macroscopic scars and remained identifiable up to 90 DPL (Fig. 1.6.). Regressing, unovulated follicles could be distinguished from POFs by histological changes in tissue morphology. The central mass of an unovulated follicle generally retained a mature primary oocyte, which was surrounded by thin, vitelline membrane (Fig. 1.6.). The connective tissue surrounding unovulated follicle walls maintained an internal and external thecal layer consisting of dense elastic and collagenous fibers. Regressing, unovulated follicles could also be distinguished from POFs by their intact mesothelium layer and spherical shape (Fig. 1.6.). Under microscopic examination, POFs were more elliptically shaped compared to round unovulated follicles and formed 3 distinct tissue layers consisting of: (1) theca interna, (2) theca spongiosa, and (3) theca externa (Fig 1.7.; Payne 1966).

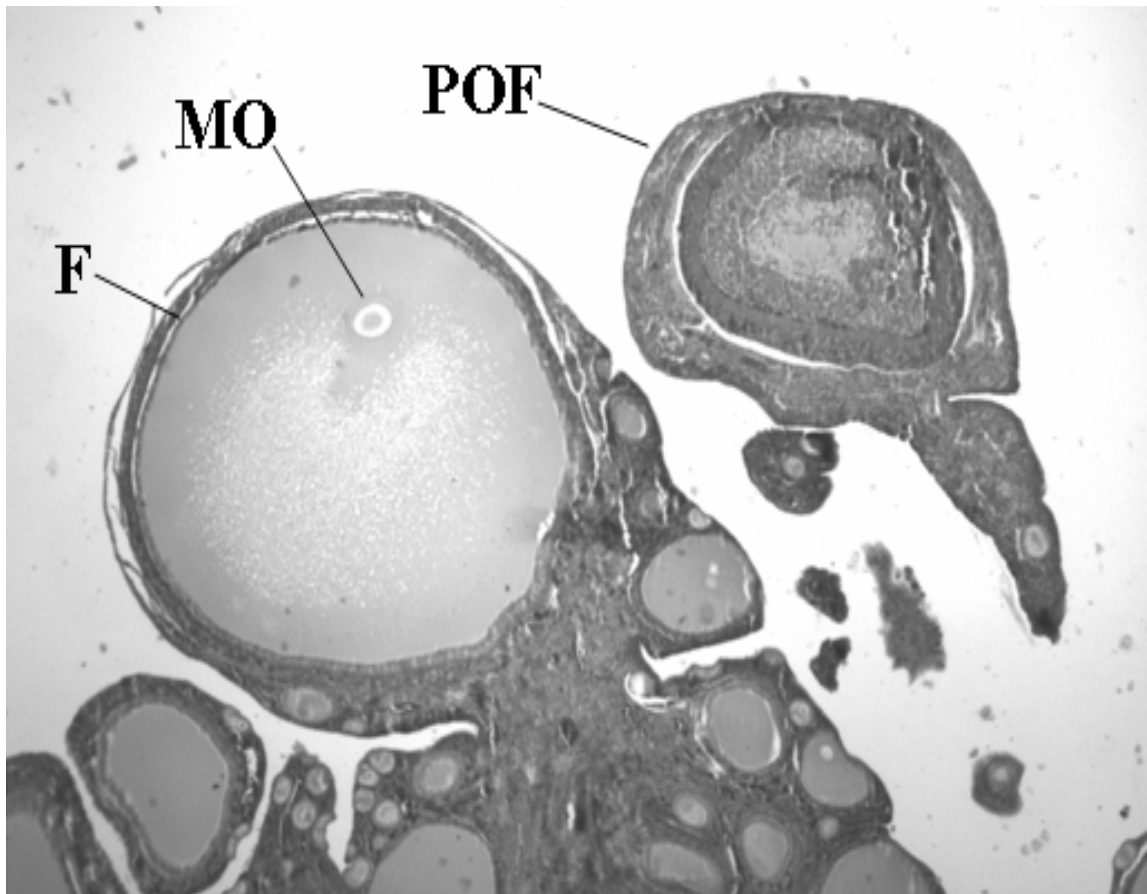


Figure 1.6. Cross-section of a mallard ovary viewed under a compound microscope (40X magnification). Note the dissimilarities between a regressing, unovulated follicle (F) compared to a remaining postovulatory follicle (POF). The regressing, unovulated follicle retained a mature primary oocyte (MO).

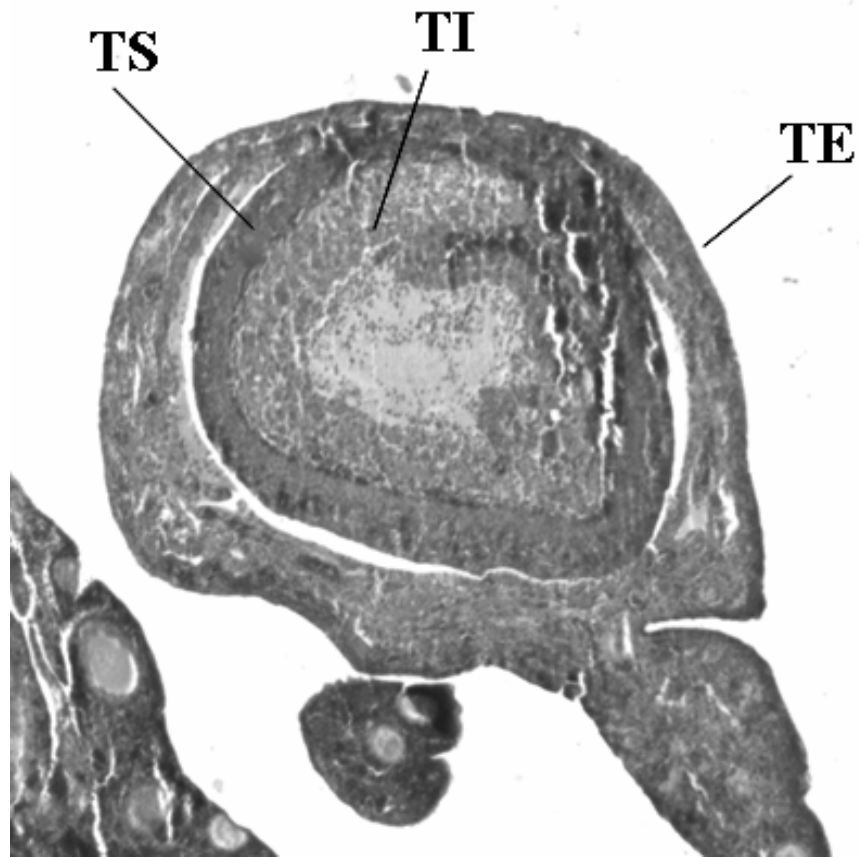


Figure 1.7. Postovulatory follicle (POF) viewed under a compound microscope (100X magnification). Note the cell wall collapse, separation, and formation of 3 distinct tissue layers. TS = theca spongiosa, TI = theca interna, and TE = theca externa as described by Payne (1966).

POF and Clutch Size Comparisons

I found a weak, marginally significant correlation between macroscopic POF counts and apparent clutch size for hens collected at 30-60 DPL (Fig. 1.8A), but not for females collected at 61-90 DPL (Fig 1.8B). POF counts and clutch size were identical for 4 of 48 (8.3%) hens, all of which were collected between 30-45 DPL (Appendix B.). Macroscopic POF counts exceeded apparent clutch estimates in 6 of 48 (12.5%) hens; 3 differed by 1 egg, 2 differed by 2 eggs, and 1 differed by 5. Most overestimates occurred in either WTHs or FRHs (5 of 6; 83.3%), with only 1 in a CBH (Appendix B.). POF counts were considerably lower than apparent clutch size estimates for the vast majority of females (Appendix B.).

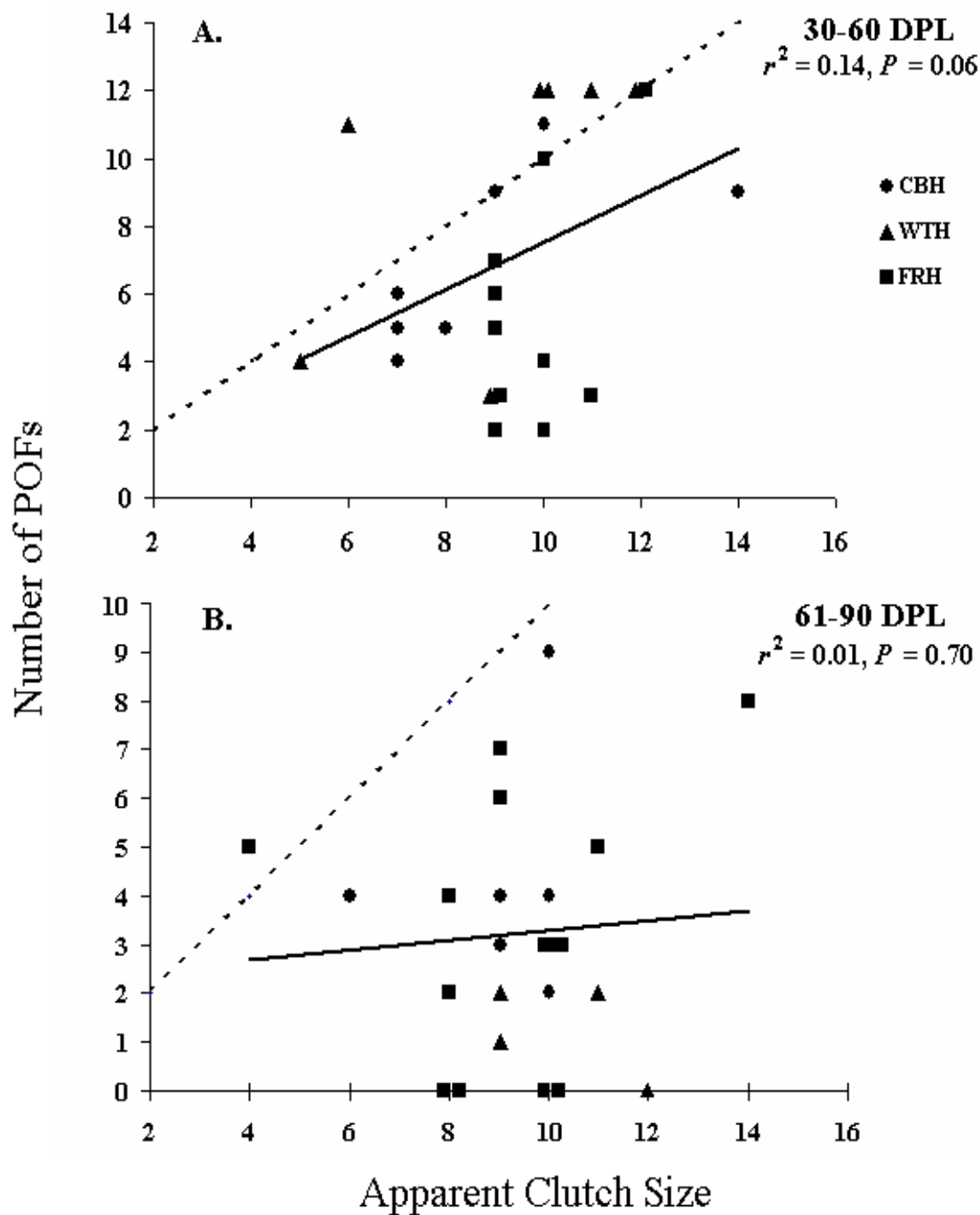


Figure 1.8. Least squares regression of macroscopic postovulatory (POF) counts on apparent clutch size for mallard ovaries collected at (A) 30-60 and (B) 61-90 days post-laying during 2002-03. Dashed line denotes a 1:1 concordance between POF counts and apparent clutch size. Circles = Captive breeding hens (CBH), Triangles = Wild-trapped hens (WTH), and Squares = Free-ranging hens (FRH).

DISCUSSION

POF EXAMINATION

Postovulatory follicles remained macro- or microscopically distinguishable up to 90 days following the completion of egg-laying in mallard females. The number of POFs and length of time they remained macroscopically discernable, however, varied among hens. For example, POFs were macroscopically conspicuous in all hens collected between 30-60 DPL, but not at periods ranging from 61 to 90 DPL. Nearly 80% of females collected between 61-90 DPL, however, retained the presence of ≥ 1 POFs, and this pattern was consistent for all laying groups. Most POFs were greatly regressed in size and lacked an open stigma, but could still be identified by their elongated shape and yellowish pigmentation (per. obs., Johnson 2000). Further examination of cross-sectioned ovaries revealed that POFs remained microscopically conspicuous for a much greater length of time than they could be discerned macroscopically. Using microscopic examination, POFs were identifiable in all hens that did not retain macroscopic scars up to 90 DPL. A review of existing literature indicates that this was the first study to document microscopic POFs in mallard ovaries.

Blind tests conducted by independent observers further illustrated that female laying status (i.e., breeder or non-breeder) could be determined using POF examination. However, it appears that macroscopic examination may only be used to distinguish breeding status consistently up to 60 DPL, and microscopic examination may be required at periods > 60 DPL. The fact that novice observers correctly assigned the breeding status for most, if not all, females also demonstrates that individuals without extensive

training can effectively use this technique. Storm misidentified 2 breeding hens as non-breeders, but these hens were collected at 63 and 75 DPL. I suspect these errors resulted from the rapid regression of ovarian follicles that occurred at periods > 60 DPL, making it difficult to distinguish breeding status in some hens (Fig. 1.5.).

EFFECTS OF CAPTIVITY

Captivity had little apparent impact on hen nesting behaviors or the ability to identify POFs. I found no difference in mean clutch size among CBHs (8.92 ± 0.55 SE), WTHs (9.45 ± 0.59 SE), or FRHs (9.45 ± 0.40 SE). Clutch size for CBHs was also consistent with findings from 20 other studies conducted on mallards throughout North America ($\bar{x} = 8.72$, range 5.7 to 10.6; Drilling et al. 2002) and for captive mallards at Delta during previous years ($\bar{x} = 9.45 \pm 0.5$ to 10.3 ± 0.3 , Batt and Prince 1979). In addition, fresh egg weights were comparable to published values from other captive (Batt and Prince 1978, 1979, Eldridge and Krapu 1988, Rhymer 1988) and free-ranging mallard hens (Lokemoen et. al. 1990 *in* North Dakota, Pehrsson 1991 *in* California).

Nesting phenology of CBHs was also similar to behaviors found in the wild. Most CBHs constructed a nest bowl 2-3 days prior to egg laying and the first eggs were laid within 4 days following isolation. Similar laying behaviors have also been documented in wild nesting hens (Coulter and Miller 1968, Sowls 1955). Although laying rates of CBHs were slightly lower (0.82 ± 0.04 eggs/day) than that assumed for wild nesting females (1 egg/day; Alisauskas and Ankney 1992), these differences were negligible. However, CBHs began laying eggs approximately 28 days later (31 May \pm

1.4, $n = 13$ compared to 3 May ± 1.4 , $n = 56$) than observed by Batt and Prince (1979). I speculate that this was due to cold spring temperatures, which have been shown to delay the onset of breeding in wild nesting females (Johnson et al. 1992). Low mean daily temperatures ($\bar{x} = 8.0 \pm 1.1$ C, range -5.6 to 28.2) in May also prevented the isolation of pairs outdoors until early May (K. Ward, pers. comm.). Despite having to isolate pairs in late spring (26 May), the range of nest initiations by CBHs (27 May to 9 June) did not differ from wild mallards at other mid-latitudes. Greenwood et al. (1995) found that nest initiation dates for free-ranging mallards in central Canada ranged from 15 April - 18 June and similar mallard nest initiations have been reported in North Dakota (Cowardin et al. 1985, Lokemoen et al. 1990, Krapu 2000). Therefore, nesting activities occurred well within the range of dates typically observed in prairie-nesting mallards.

Nearly all CBHs (92.3%; 12 of 13) incubated their clutch for 23-27 days, which is consistent with wild-nesting females ($\bar{x} = 28$ days, range 23-30 days; Drilling et al. 2002). Nest abandonment occurred in only 2 CBHs, but previous research at Delta has also shown that some captive mallards will desert their nest during mid-incubation (Batt and Prince 1978,1979). Overall similarities in clutch size, nesting phenology, and incubation behavior suggest that CBH nesting activities were similar to behaviors observed in the wild. Thus, it appears that maintaining hens in captivity had little to no impact on laying behaviors and should not have affected POF persistence.

In addition, WTHs exhibited minimal changes in body mass between the time of capture and euthanasia. These birds also began feeding on provided diets within 24-36 hrs following isolation. These data suggest that females acclimated well to captive

conditions and changes in body mass that could have affected POF envelopment were likely negligible. Laying behaviors, nesting chronology, and nest fate recorded for FRHs were also comparable to findings from other studies conducted on free-ranging hens in California (McLandress et al. 1996, Loughman et al. 2004). Because a representative sample of these birds were collected at various post-laying periods, I would not expect POFs persistence to differ from other females breeding within the Sacramento Valley of California. Finally, I found no difference in the proportion of females that retained ≥ 1 macroscopic POFs among laying groups (Table 1.6.). The combination of these findings suggest that maintaining females in captivity had little to no effect on the ability to identify POFs.

POF PERSISTENCE AND RELATIONSHIP TO CLUTCH SIZE

Although several studies have examined POFs in waterfowl (e.g., Wood 1964, Ankney 1974, Krapu 1974, Afton 1984, Ankney and MacInnes 1978, Barzen and Serie 1990, Semel and Sherman 1991, Mann and Sedinger 1993, Young 1993, Esler 1994, Esler and Grand 1994, Hohman and Crawford 1995, Hohman et al. 1996), few have determined how long these structures persist following the breeding season. The relatively few studies that have examined POF persistence in waterfowl suggest that these structures regress rapidly and can be used to estimate clutch size for a short period of time following ovulation (Krapu 1974, Semel and Sherman 1991, Esler 1994). Semel and Sherman (1991) found that POFs were not detectable only 30 days following ovulation in female wood ducks. It is important to note that these results were based on a

small sample of females ($n = 5$), and therefore, may not represent what is true for all post-breeding wood ducks. Esler (1994) hypothesized that POFs regress at similar rates in northern pintail, American wigeon, and lesser scaup, but did not actually quantify whether these scars remain for an extended period of time (i.e., > 30 DPL).

Contrary to the conclusions of these studies, residual portions of POFs do appear to persist for a much greater length of time in some waterfowl species. For instance, POFs remain recognizable until the end of incubation in black brant and lesser snow geese (Barry 1962, Ankney 1974). Using macroscopic POF counts, Ankney (1974) correctly estimated clutch size in 67 of 75 (88%) female lesser snow geese for periods up to 24 DPL. Miscalculations in some females (8 of 75; 12%) were likely due to inaccurate estimates of clutch size resulting from partial clutch depredation or nest parasitism, and therefore, did not necessarily indicate errors in POF counts. Similarly, I found that POFs remain discernable in mallards for a considerable length of time following the completion of egg laying. My findings are also consistent with Lofts and Murton (1973:45) and Johnson (2000:571) who suggested that residual portions of POFs may persist up to several months in post-breeding mallards.

I found no relationship between macroscopic POF counts and clutch size (Fig. 1.8.), but these results were not surprising. All ovaries examined in this study were collected 1-3 months following the completion of egg laying, which is considerably later than most previous studies (e.g., Ankney 1974 ≤ 24 DPL, Semel and Sherman 1991 ≤ 30 DPL, and Esler 1994 < 30 DPL). Also, because POFs regress rapidly in waterfowl (Bluhm 1992), I would not predict a strong relationship between POF counts and clutch

size at later post-laying periods. Apparent clutch size and POFs counts were identical in only a small fraction of hens (4 of 48; 8.3%), all of which were collected between 30-45 DPL. There did, however, appear to be a much stronger association between POF counts and clutch size for hens collected between 30-60 DPL compared to 61-90 DPL (Fig. 1.8.). These results are consistent with Arnold (1990) who found no correlation between macroscopic POF counts and clutch size in post-laying American coots (*Fulica americana*) shortly following egg laying. Arnold hypothesized that this was due to the rapid regression of POFs, but may have also resulted from inaccurate estimates of clutch size (i.e., exact laying histories of females were not known). Arnold et al. (1997) later noted that evidence of egg laying can still be determined in incubating coots using macroscopic POFs, despite finding a weak concordance between POF counts and clutch size. My results confirm the same is true for post-breeding mallards.

Macroscopic POF counts exceeded apparent clutch size in 6 of 48 (12.5%) hens, 5 of which differed by only 1-2 eggs and one of which differed by 5 eggs (Appendix B.). Most overestimates occurred in either wild-trapped (4) or free-ranging hens (1). A number of plausible mechanisms could have resulted in overestimates of clutch size. For example, nest parasitism, re-nesting, and/or partial clutch depredation may have produced differences in actual versus apparent clutch size observed at the time of hen capture. Therefore, apparent clutch size for both WTHs and FRHs did not necessarily indicate the actual number of eggs laid, but rather indicated that egg laying occurred and at approximately what time during the breeding season. In contrast, I found that POF counts exceeded apparent clutch size in only 1 of 13 (7.7%) captive breeding females,

which differed by 1 egg. I suspect this disparity may have simply resulted from inadvertently counting 1 POF twice, and did not necessarily imply errors in POF identification.

Misidentification of atretic follicles as POFs can also result in overestimates of clutch size (Meyer et al. 1947, Davis 1942*b*, Payne 1965, Arnold et al. 1997). Payne (1965) suggested that the occlusion of an open stigma, loss of yellow pigmentation, and regression of follicle size often makes it difficult to distinguish between POFs and atretic follicles at later stages of envelopment. Although the majority of POFs found in this study had an occluded stigma (filled with cream-colored phagocytes and granulosa cells), they could still be identified by their yellowish pigmentation characteristic of terminal involution (Lewin 1963, Johnson 2000). Atresia can occur when large yolk-filled follicles or pre-ovulatory follicles are reabsorbed prior to ovulation and two types are common in birds: (1) involution and (2) bursting (Johnson 2000). Involution atresia occurs when the oocyte and yolk are enveloped into the ovary and the follicle becomes discolored and irregularly shaped. During bursting atresia, ovarian follicles rupture and their yolk contents are released into the body cavity (Scott and Ankney 1983, Johnson 2000, Curson and Mathews 2003).

Ovarian follicles that enter rapid follicle growth rarely undergo atresia (Johnson 2000), and hence misidentifying atretic follicles as POFs was not likely a confounding issue in this study. Atretic follicles also appear much less prevalent in some bird species such as ring-necked pheasants (*Phasianus colchicus*; Meyer et al. 1947) and most waterfowl (Arnold et al. 1997). Atresia is common, however, in some arctic nesting

geese that reduce nutrient allocation to the ovary for maintenance costs during delayed nesting seasons (Barry 1962, Hamann et al. 1986). Finally, even recently ovulated POFs do not always directly correspond to the exact number of eggs laid. Some ova released into the peritoneal cavity of birds may not reach the oviduct for development and eventually get reabsorbed (Meyer et al. 1947).

I found that POF counts underestimated clutch size in the majority of females and these findings were consistent for all laying groups (Appendix B.). The rapid envelopment of POFs following ovulation was likely responsible for underestimations or diminutive scars may have simply been overlooked. I must emphasize, however, that the focus of this study was not to estimate clutch size in mallards using POFs, but rather to determine whether egg laying occurred during the most recent breeding season. Similarly, Meyer et al. (1947) found that POFs could not be used to accurately estimate clutch size for > 15 days following ovulation in pheasants, but noted that some of these scars will remain for several months (see also Buss et al. 1951). Hannon (1981) stated that macroscopic examination of POFs could also be used to determine the breeding status of hunter-harvested blue grouse (*Dendragapus obscurus*), even though these structures were not a reliable indicator of clutch size. My results demonstrate that POF examination may be used to indicate recent egg production in mallards up to 2-3 months following the completion of egg laying.

IMPLICATIONS AND FUTURE CONSIDERATIONS

Breeding probability is difficult to accurately measure in mallard populations and its influence on population dynamics remains unclear. My results suggest that POF examination may provide a useful approach to estimate breeding probability in mallard populations. Previously, researchers have radio-marked a large number of pre-breeding females to evaluate reproductive parameters in mallards (Gilmer et al. 1974, Cowardin et al. 1985, Pietz et al. 1993, Rotella et al. 1993, Paquette et al. 1997), but these types of projects are often costly and logistically difficult. Radio-marking pre-breeding females may adversely impact breeding behavior (e.g., Pietz et al. 1993, Rotella et al. 1993, Paquette et al. 1997) and current methods used to capture hens prior to radio-attachment likely exclude a large component of non-breeders. Therefore, radio-telemetry studies may not be an optimal approach to estimate breeding probability in mallards or other waterfowl species. Instead, the development and adoption of POF examination may provide more accurate estimates of this important vital rate. Applying this technique to unmarked females would remove confounding effects associated with “trapping bias” and potential physiological impacts caused by radio-transmitter attachment.

This method may be well suited for mallards breeding within the Sacramento Valley of California for a number of reasons. Unlike prairie-nesting mallards, breeding and non-breeding females inhabit similar geographic areas and habitats due to their non-migratory nature. This may allow researchers to collect a more representative sample of both breeding and non-breeding hens at a landscape scale. Ideally, it would be most informative to apply this technique to hunter-harvested birds, but I am unsure whether

POFs persist long enough for this approach (i.e., > 90 DPL). Instead, researchers would most likely need to randomly collect females 2-3 months following the breeding season.

Theoretically, researchers could use nest initiation data for a particular year to design a collection regime. To illustrate, previous research has shown that females within the Sacramento Valley first complete egg laying by approximately the first week in March and 95% of hens complete egg laying by approximately 27 May (McLandress et al. 1996; Fig. 1.9A). Hens rarely initiate nests after this date (McLandress et al. 1996, S. Oldenburger, unpub. data). Assuming that 95% of nesting hens incubate for 27-30 days, researchers could collect hens around 26 June (177 Julian days; Fig. 1.9B) from a variety of habitats that birds would likely inhabit (e.g., flooded rice fields, brood rearing ponds, irrigation ditches, seasonal wetlands, etc.). By this date, females would have either: (1) successfully hatched a brood, (2) failed at nesting, or (3) not attempted to nest. Because 26 June is \leq 90 DPL for 90-95% of hens in the Sacramento Valley, a combination macro- and microscopic examination would allow researchers to reliably estimate breeding probability in this population (Fig. 1.9B). Granted, a key assumption of this sampling design is that a representative sample of both breeding and non-breeding females are collected.

When collecting hens, researchers must also take into account a number of demographic and environmental variables that could affect breeding probability estimates. For example, previous research in California has shown that some post-breeding mallard females will migrate to portions of northern California and southern

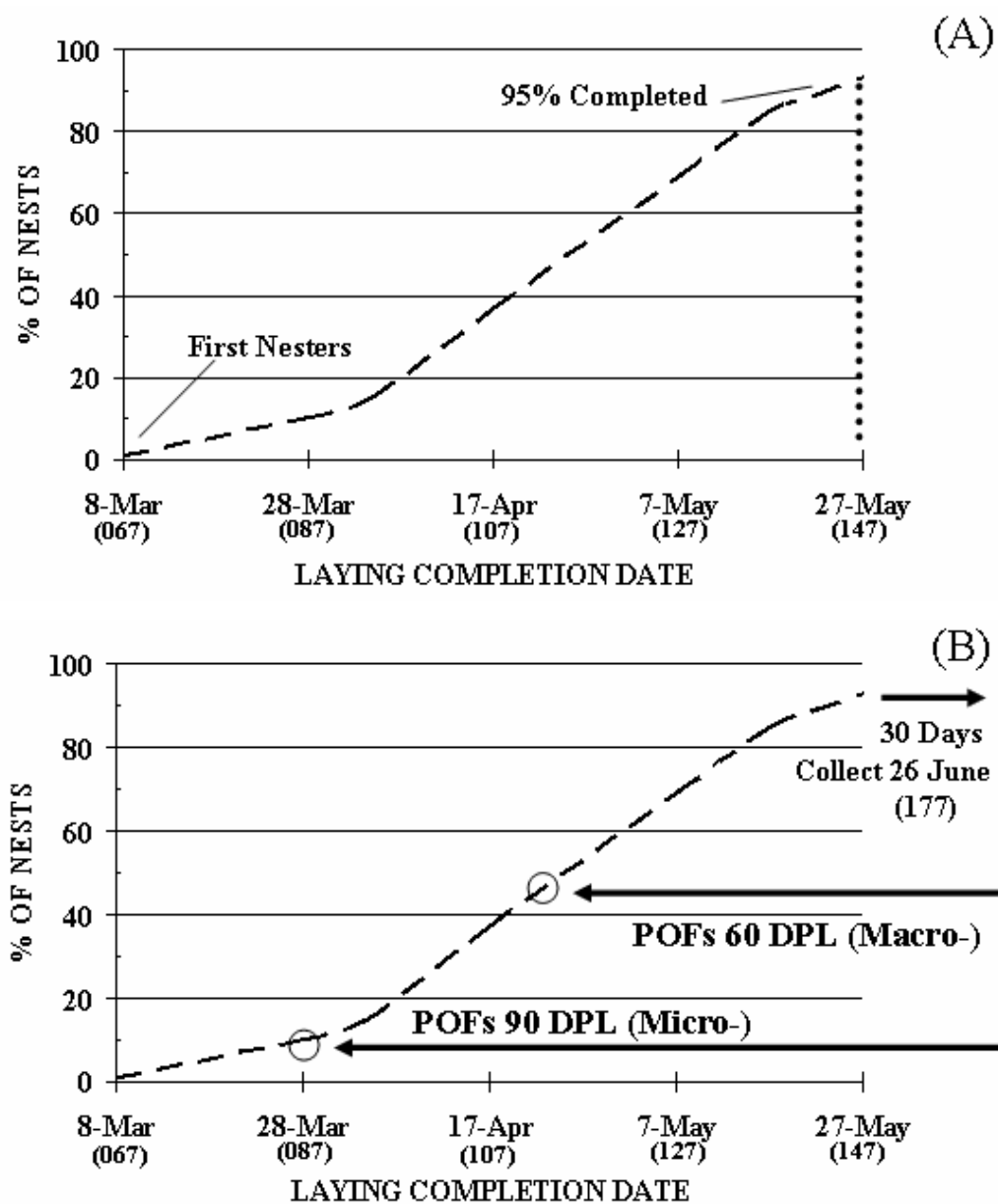


Figure 1.9. Schematic representation illustrating a potential collection schedule used to estimate breeding probability of mallards breeding within the Sacramento Valley of California. Nest phenology dates adapted from data collected by McLandress et al. (1996). (A) Percentage of hens which have completed egg laying as a function of time. (B) Collection and back-calculation dates used to estimate breeding probability using macro- and microscopic examination techniques.

Oregon in late-May and June to molt (Yarris et al. 1994). Therefore, collecting females from key molting areas, such as the Klamath Basin (Yarris et al. 1994), during summer may be important. Combining age-structure to these data may also allow researchers to determine age-specific (second-year versus after-second-year) differences in mallard breeding probabilities.

In addition to spatial variation, breeding probability estimates would also vary annually. Weather variables, such as temperature and spring precipitation, play a key role in California mallard breeding efforts (Earle 1950, Mayhew 1955, McLandress et al. 1996). Thus, collecting females during multiple years would be required to account for annual variation in breeding probability estimates due environmental stochasticity (i.e., wet versus dry years). Using this technique, researchers could also examine differences in breeding probability estimates as a function of individual quality. Potentially, these results could indicate that a large proportion of non-breeding individuals (i.e., those without POFs) are in poorer body condition compared to breeding hens (i.e., those with POFs). If so, this would support the hypothesis that nutrient availability greatly impacts California mallard breeding efforts and recruitment. Clearly, continued investigation is needed to develop a collection regime that would account for both spatial and temporal heterogeneity in breeding probability estimates.

Although this technique was developed primarily for California mallards, it should be applicable to other regional populations, such as those breeding within the Prairie Pothole and Great Lakes Regions. Using POFs to determine breeding status may be especially useful because mallards within these areas have a much shorter nesting

season compared to California birds. The success of this technique, however, depends largely on the ability to randomly sample birds, which may be much more difficult in migratory populations. For prairie-nesting mallards, one potential strategy may be to collect females from large molting areas or areas prone to severe botulism outbreaks during mid-summer. Collecting hens throughout the nesting season from these areas may provide a random sample of individuals from the surrounding landscape. Continued investigation is needed to examine differences in post-breeding movements and habitat utilization between breeding and non-breeding females. Progress in these areas will improve our ability to develop appropriate sampling designs to collect females at a landscape scale.

To adequately model mallard population dynamics, an unbiased estimate of breeding probability is needed. Obtaining more accurate estimates will greatly enhance our understanding of mallard population dynamics, and aid in the future construction of more robust population models. Increased knowledge regarding the relative impact that breeding probability has on waterfowl productivity is vital for proper and cost-effective management decisions. Clearly, understanding the influence breeding probability has on mallard recruitment in California and in other regions, warrants further research. Finally, the development and success of this technique may lead to future studies addressing breeding probability estimates and reproductive limitations in other waterfowl populations of interest, such as northern pintail and scaup.

CHAPTER 2: FACTORS INFLUENCING OVARY REGRESSION AND POSTOVULATORY FOLLICLE ENVELOPMENT IN MALLARDS

INTRODUCTION

Postovulatory follicles have been commonly used to indicate egg production (Davis 1942*a*, Hannon 1981), measure brood parasitism (Kennedy et al. 1989), and estimate clutch size for a variety of birds (Davis 1942*b*, 1958, Kabat et al. 1948, Buss et al. 1951, Payne 1973, Scott and Ankney 1983, Arnold et al. 1997, Pearson and Rohwer 1998, Curson and Mathews 2003, Dolbeer and Bernhardt 2003). Numerous studies have also used POFs to determine stage of breeding and to assess nutrient reserve commitments to clutch formation in laying waterfowl (Alisauskas and Ankney 1992, Mann and Sedinger 1993, Young 1993, Esler and Grand 1994, Petrie and Rogers 2004). The length of time POFs remain distinguishable following ovulation, however, differs considerably among avian taxa (see Semel and Sherman 1991 for review).

For example, POFs remain identifiable for less than 10 days post-laying (DPL) in California quail (*Callipepla californica*; Lewin 1963), but can persist up to several months following ovulation in blue grouse (Standing 1960; but see Hannon 1981) and captive ring-necked pheasants (Meyer et al. 1947, Kabat et al. 1948). As in Gallinaceous birds, the length of time POFs remain conspicuous also differs among waterfowl species. Semel and Sherman (1991) found that POFs were not detectable 30 days following ovulation in female wood ducks and Esler (1994) hypothesized that POFs persist for a similar period of time (i.e., < 30 DPL) in subarctic nesting northern pintail, American wigeon, and lesser scaup. In contrast, POFs have been used to estimate clutch size accurately up to 24 DPL in female lesser snow geese (Ankney 1974) and may persist up

to several months in mallards (Lofts and Murton 1973:45, Johnson 2000:571). Although POF examination in birds dates back over two centuries (Jenner 1788), relatively few studies have investigated factors that influence POF envelopment rates. Understanding the environmental, physiological, and social factors that regulate reproduction and POF envelopment in breeding waterfowl, however, is of paramount importance (Bluhm 1992).

Previous studies have suggested that body condition, stage of breeding, and clutch size can affect POF envelopment in female ring-necked pheasants (Meyer et al. 1947, Kabat et al. 1948). Arnold et al. (1997) further hypothesized that the onset of incubation, and subsequent rise in prolactin levels can accelerate POF envelopment in American coots. Differences in yolk size (Jull 1934), delayed ovulation (Scott and Warren 1936), and the period of time between laying sequences (Phillips 1936) are thought to affect POF envelopment rates in domestic fowl. A number of ultimate (e.g., climate, food availability, social behaviors, etc.) and proximate factors (e.g., hormone levels) can also influence reproductive function and gonad development in breeding birds (Lofts and Murton 1973, Bluhm 1992, Johnson 2000). The fact that POFs envelop rapidly following ovulation has been widely recognized in a number of waterfowl species (Krapu 1974, Semel and Sherman 1991, Bluhm 1992, Esler 1994), but few studies have assessed specific factors that influence POF envelopment rates (but see Esler 1994). In other words, why do some females retain a greater number of POFs for a longer period of time than others?

To address this lack of information, I investigated the potential influence of various ecological and physiological aspects on POF envelopment rates in female

mallards. Specifically, I examined the effects of: (1) captive conditions; (2) days post-laying; (3) body condition; (4) age, (5) ovary weight; (6) clutch size; and (7) brood rearing on POF envelopment. Based on previous studies, I developed a series of *a priori* predictions regarding how these variables could affect POF envelopment.

First, I predicted that the number of POFs remaining may have differed among laying groups due to physiological impacts caused by maintaining hens in captivity. Because POFs regress rapidly following ovulation in waterfowl (Semel and Sherman 1991, Bluhm 1992, Esler 1994), I predicted that the number of POFs remaining would decrease significantly with increasing DPL. Second, I predicted an positive relationship between the number of POFs remaining and ovary weight (i.e., ovaries with a larger mass or those less regressed would have more POFs remaining). I also predicted a positive correlation between the number of POFs remaining and clutch size because hens that lay large clutches typically invest more nutrient reserves into breeding efforts (Alisauskas and Ankney 1992), and therefore would most likely have a greater number of POFs remaining. Similarly, I hypothesized that older, more experienced females and those hens in better condition would have more POFs remaining compared to younger hens and those in poorer body condition. Finally, because brood behavior (i.e., rise in prolactin levels) can accelerate ovary regression in waterfowl (Bluhm 1992), I predicted a inverse relationship between the length of time (days) hens were with a brood and the number of POFs remaining.

METHODS

DATA COLLECTION

Mallard Ovaries and Reproductive Parameters

Ovaries were collected from 48 post-breeding mallard hens at periods ranging from 30-90 days following the cessation of egg laying. Ovaries were removed from 24 captive females (13 CBHs, 11 WTHs) maintained at the Delta Waterfowl Research Station Research and 24 radio-marked, FRHs breeding within the Sacramento Valley of California. One FRH (172.571) was censored from all subsequent analysis due to her emaciated condition.

I recorded apparent clutch size, incubation behavior, and nest success for each hen. Laying cessation dates were also calculated following methods described in Chapter 1. All WTHs were captured from the nest during incubation, and did not successfully hatch their clutch. Ducklings were also removed from CBHs immediately following hatch. I was able to determine how long FRHs were with a brood (BROODDAYS) based on hen behavior, although their ducklings were not fitted with radio transmitters. I verified brood survival by visually locating brood hens at 1-2 week intervals. I concluded that total brood loss occurred if a hen was observed without ducklings, paired with a drake, or moved long distances (>1,000 m) on a regular daily basis. If a hen was observed with a brood on one date (e.g., 18 June) and not a subsequent date (e.g., 22 June), I assumed that the brood survived until the intervening midpoint (e.g., 20 June). All hens were later euthanized (CBHs and WTHs) or collected via a shotgun (FRHs) at

30-90 DPL. Detailed methods regarding the experimental design and collection of birds are provided in CHAPTER 1.

Laboratory Processing

I recorded a series of structural measurements from each hen to construct an index of body condition (Dufour et al. 1993, Robb 2002). I measured culmen, tarsus, skull, and keel length with an electronic caliper (± 0.01 mm); wing chord using a flat-edge rule (± 1 mm); and body mass using an electronic balance (± 1.0 g). Hens were also aged as second-year (SY) or after-second-year (ASY) birds using wing feather characteristics (Krapu 1979). Ovaries were then removed, weighed (± 0.01 g), and fixed in 10% buffered formalin. Excised ovaries were later examined under a 6.4-16X dissecting microscope (with no prior knowledge of laying histories) and the number of POFs counted was recorded. Obvious POFs were identified by their flattened/elongated shape and open stigma (Davis 1942*a*), but most POFs were identified as yellowish follicles having an occluded stigma characteristic of the terminal involution (Lewin 1963, Scott and Ankney 1983, Pearson and Rohwer 1998, Curson and Mathews 2003). I distinguished unovulated follicles from POFs as: (1) follicles that had prematurely ruptured in areas other than the stigma (i.e. atretic follicles), or (2) smooth spherical follicles having an opaque appearance (Johnson 2000).

STATISTICAL ANALYSIS

Clutch Size, Structural Size, and Body Condition

I compared differences in apparent clutch size among separate laying groups (CBH, WTH, and FRH) using a one-way ANOVA (PROC GLM), following tests to ensure data were normally distributed (PROC UNIVARIATE NORMAL). I also calculated estimates of female body condition by adjusting body mass (g) for variation in structural size and stage of breeding. First, to correct for variation in structural size, I conducted a principal component analysis (PROC PRINCOMP) based on the correlation matrix of 5 structural measurements (culmen, tarsus, skull, keel, wing chord). The first principal component (PC1) described a positive relationship among all structural measurements and accounted for 50.5% of the variation among original measures. Thus, I was able to use the PC1 score as an overall index of structural size for each hen. Previous research has also shown the mallard mass varies seasonally (Dufour et. al 1993, Robb 2002); therefore, I controlled for seasonal variation in female mass using the following general linear model:

$$Y_{ij} = \beta_0 + \beta_1 \text{GROUP} + \beta_2 \text{PC1} + \beta_3 \text{DPL} + \beta_4 \text{GROUP} * \text{DPL} + \epsilon_{ij},$$

where Y_{ij} is female mass (g) at collection, β_0 is the regression coefficient, $\beta_1 X_1$ is laying group (GROUP), $\beta_2 X_2$ is structural size (PC1), $\beta_3 X_3$ is the number of days post-laying (DPL), $\beta_4 X_4$ is a GROUP*DPL interaction, and ϵ_{ij} refers to an associated error term.

Differences in adjusted female mass (body condition hereafter) and structural size (PC1 Score) were compared among laying groups using a *post hoc* Tukey's HSD test (Sokal and Rohlf 2000).

Ovary Regression and POF Envelopment

Maintaining hens in captivity may have affected ovary regression and POF envelopment rates. Thus, I used an analysis of covariance (ANCOVA; PROC GLM) to test for differences in ovary weight (± 0.01 g) among laying groups after controlling for effects of DPL, and a GROUP*DPL interaction. Individual means were adjusted (LS means) and compared using Tukey's HSD test. Simple linear regression (PROC GLM) was also used to simultaneously assess the influence of BROODDAYS and DPL on the number of POFs remaining for free-ranging hens. I was unable to test the impact of BROODDAYS on POF envelopment for CBHs or WTHs because these females were either separated from their ducklings immediately following hatch or were removed from their clutch prior to hatch.

Finally, I developed *a priori* candidate models to describe the influence of various factors on the number of POFs remaining. Candidate models included the effects of female age (AGE), ovary weight (OWEIGHT), clutch size (CLUTCH), body condition (BCOND), days post-laying (DPL), laying groups (GROUP), and all 2-way interactions. I selected among competing models using Akaike's Information Criteria corrected for small sample sizes (AIC_c) and the model with the lowest AIC_c value was considered the most parsimonious (Burnham and Anderson 1998). I calculated AIC_c differences (ΔAIC_c) and Akaike weights (w_i) as a measure of evidence supporting the best model. All analyses were performed using SAS version 8.0 software (SAS Institute 1999) and considered statistically significant at $P \leq 0.05$.

RESULTS

CLUTCH SIZE AND POF COUNTS

Mean apparent clutch size did not differ significantly ($F_{2,45} = 0.35$, $P = 0.71$) among captive ($\bar{x} = 8.92 \pm 0.55$ SE, $n = 13$), wild-trapped ($\bar{x} = 9.45 \pm 0.59$ SE, $n = 11$) or free-ranging ($\bar{x} = 9.35 \pm 0.36$ SE, $n = 23$) hens. Examination of excised ovaries revealed that ≥ 1 POFs remained conspicuous in 42 of 47 (89.4%) hens collected between 30-90 DPL. Only 5 of 47 (10.6%) females did not retain POFs and these were collected at 61, 65, 70, 71, and 75 DPL (Appendix B.). Postovulatory follicles were recognizable in all CBHs (13 of 13) and in most WTHs (90.9%; 10 of 11) and FRHs (82.6%; 19 of 23). POFs also remained discernable in all females collected between 30-60 DPL, and in 79.2% (19 of 24) females collected between 61-90 DPL (Appendix B.)

STRUCTURAL SIZE AND BODY CONDITION

Captive breeding females were significantly larger in structural size (i.e., higher PC1 value; $P < 0.001$) than both WTHs and FRHs, but I found no significant difference ($P = 0.71$) in structural size between WTHs and FRHs (Table 2.1.). Results of the multiple regression model were highly significant ($F_{6,40} = 11.04$, $P < 0.0001$) indicating an effect of structural size (PC1), DPL, GROUP, and a GROUP*DPL interaction on female body mass (Table 2.2.). Post hoc comparisons using Tukey's HSD, however, indicated that body condition estimates did not differ significantly among laying groups (Table 2.1.).

Table 2.1. Mean adjusted body mass (g) and structural size comparisons of mallard hens ($n = 47$) collected at 30-90 days post-laying, 2002-03. Tukey's test used for multiple pair-wise comparisons among groups. Groups sharing the same letter were not significantly different ($P > 0.05$) from each other.

Group	n	Body Condition		Structural Size	
		Body Mass (\pm SE)	Tukey's	PC1 Score (\pm SE)	Tukey's
Captive	13	966.76 (20.18)	A	1.44 (0.37)	A
Free-Ranging	23	934.09 (13.78)	A	-0.68 (0.27)	B
Wild-Trapped	11	915.27 (19.04)	A	-0.29 (0.40)	B

Table 2.2. General linear model of the influence of laying group (GROUP), structural size (PC1), and days post-laying (DPL) on body mass of post-breeding mallard hens collected during 2002-03.

Source of Variation	DF	Sum of Squares (Type III)	F	<i>P</i> -value
GROUP	2	26,556.11	3.46	0.0411
PC1	1	93,655.60	24.40	<0.0001
DPL	1	43,662.69	11.38	0.0017
GROUP*DPL	2	15,837.14	4.13	0.0235
ERROR	40	153,527.22		

OVARY REGRESSION

Results of the ANCOVA model were highly significant ($F_{5,41} = 11.24$, $P < 0.0001$) indicating an effect of GROUP, DPL, and a GROUP*DPL interaction on ovary weight (Table 2.3.). A significant interaction between GROUP and DPL indicated that ovary regression rates differed among laying groups. Ovary mass of WTHs decreased at a slower rate than both CBHs and FRHs ($P = 0.004$; Fig. 2.1.). Post hoc comparisons using Tukey's HSD demonstrated that ovary mass was significantly greater ($P = 0.05$) in WTHs ($\bar{x} = 0.62 \text{ g} \pm 0.05 \text{ SE}$) than both CBHs ($\bar{x} = 0.48 \pm 0.04$) and FRHs ($\bar{x} = 0.43 \pm 0.03$) after controlling for variation in DPL (Fig. 2.2.). I found no difference ($P > 0.05$) in ovary mass, however, between CBHs and FRHs (Fig. 2.2.). In general, ovaries appeared to reach a quiescent (winter) state by approximately 60 DPL, and this pattern was consistent for all laying groups (Fig. 2.1.).

FACTORS INFLUENCING POF ENVELOPMENT

Of the 18 candidate models, the most parsimonious model contained DPL and OWEIGHT, which accounted for 43% of variation in the data (Table 2.4.). Adding GROUP and a GROUP*DPL interaction to this model increased the AICc value by only 1.0, and explained more of the variation in the data (54%). Female age appeared to have little to no effect on POF envelopment as indicated by the candidate model set (Table 2.4.). Female body condition and clutch size also did not appear to have a substantial impact on POF envelopment based on low model weights and high AICc values (Table 2.4.). Four of the top 6 candidate models included the effects of DPL, OWEIGHT,

Table 2.3. ANCOVA model (Ovary Weight = GROUP DPL GROUP*DPL) results used to examine the influence of laying group (GROUP), days post-laying (DPL), and a group*DPL interaction on ovary weights recorded for 47 mallard females collected at 30-90 DPL, 2002-03.

Source of Variation	DF	Sum of Squares (Type III)	F	<i>P</i> -value
GROUP	2	0.650	14.39	< 0.0001
DPL	1	0.442	19.58	< 0.0001
GROUP*DPL	2	0.450	9.96	0.0003
ERROR	41	0.926		

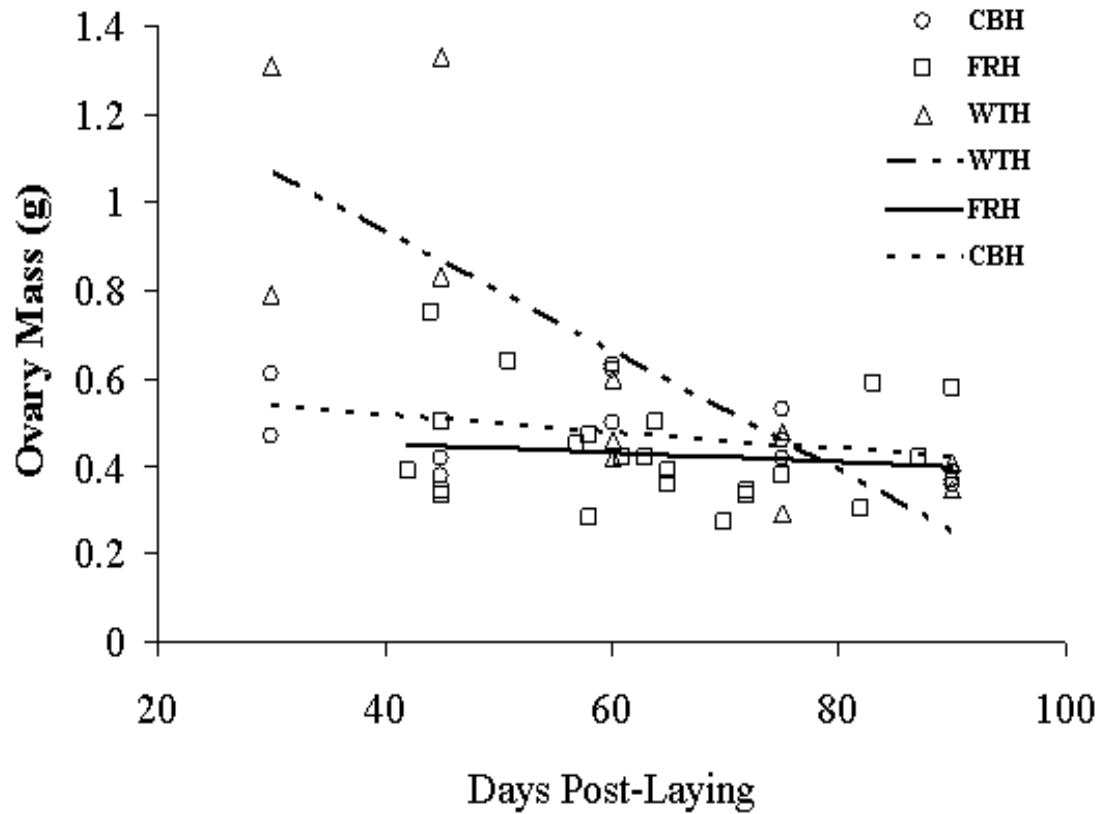


Figure 2.1. Ovary regression rates for post-breeding mallard hens collected at 30-90 days post-laying during 2002-03. CBH (circles) = Captive breeding hens ($r^2 = 0.19$, $P = 0.13$); WTH (triangles) = Wild-trapped hens ($r^2 = 0.62$, $P = 0.004$); and FRH (squares) = Free-ranging hens ($r^2 = 0.015$, $P = 0.57$). Line patterns denoted in the legend indicate ovary regression rates for each laying group.

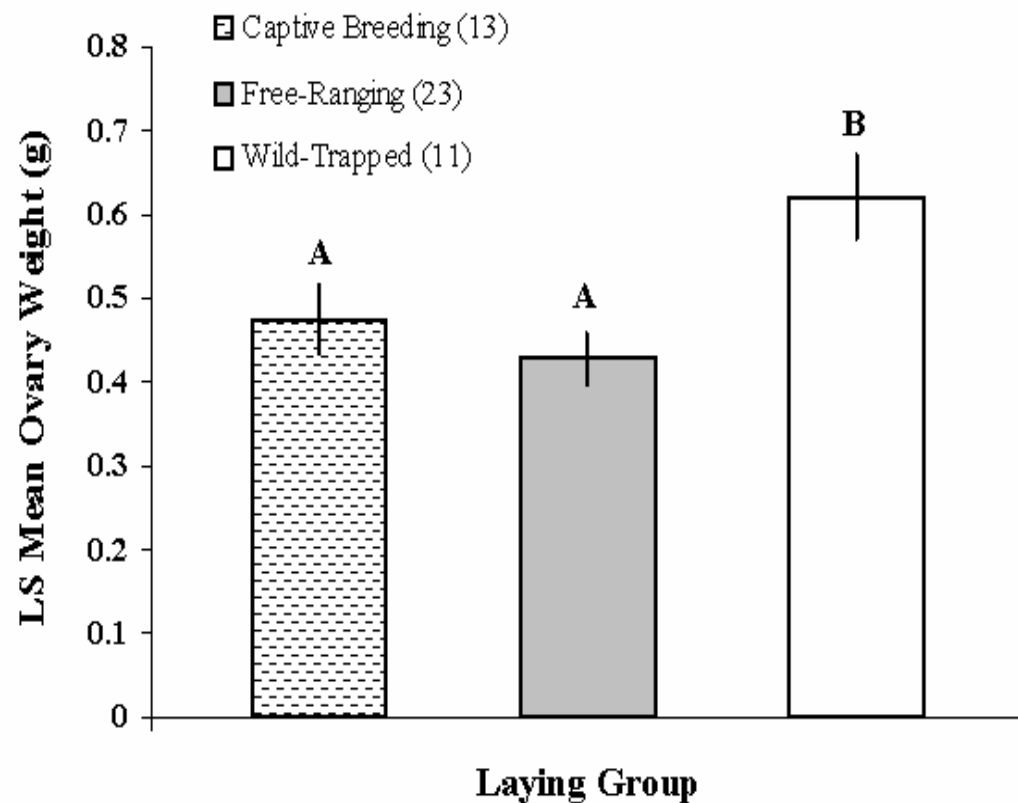


Figure 2.2. Mean adjusted ovary weight (\pm SE) comparisons made among captive breeding, wild-trapped, and free-ranging mallards collected at 30-90 days post-laying, 2002-03. Multiple pair-wise comparisons made using Tukey's test and groups with same letter indicate not significantly different. Sample sizes for each laying group denoted in parentheses.

and GROUP, which collectively accounted for almost the entire Akaike weight (Table 2.4.).

Further examination of regression coefficients indicated that the number of POFs remaining was inversely related to DPL and positively correlated with OWEIGHT. After partitioning the data further, I found that the number of POFs remaining was inversely correlated to DPL for both CBHs and WTHs maintained in captivity, but not for FRHs collected in California (Fig. 2.3.). I also found no correlation between BROODDAYS and the number of POFs remaining for FRHs collected in California ($r^2 = 0.07$, $P = 0.46$), suggesting that the length of time hens were with a brood did not appear to have a substantial impact on POF envelopment rates.

Table. 2.4. Candidate models to explain the number of POFs remaining for 47 female mallards collected at 30-90 days post-laying, 2002-03. Models evaluated using Akaike's Information Criterion for small sample sizes (AICc).

MODEL ^a	K ^b	AICc	ΔAICc	w _i ^c	R ²
DPL OWEIGHT	4	101.1	0.0	0.31	0.43
GROUP DPL OWEIGHT GROUP*DPL	8	102.1	1.0	0.18	0.54
GROUP DPL GROUP*DPL	7	102.5	1.4	0.16	0.51
GROUP DPL OWEIGHT	6	102.6	1.4	0.15	0.48
OWEIGHT	3	103.7	2.6	0.08	0.37
GROUP DPL OWEIGHT GROUP*DPL GROUP*OWEIGHT	10	104.5	3.4	0.06	0.58
AGE GROUP DPL OWEIGHT	7	105.2	4.1	0.04	0.48
AGE GROUP CLUTCH DPL OWEIGHT	8	107.5	6.4	0.01	0.49
AGE GROUP CLUTCH DPL BCOND OWEIGHT	9	110.5	9.4	<0.001	0.49
GROUP DPL	5	110.7	9.6	<0.001	0.34
DPL	3	111.6	10.5	<0.001	0.26
AGE GROUP CLUTCH DPL BCOND OWEIGHT GROUP*CLUTCH	11	116.6	15.5	<0.001	0.49
AGE GROUP CLUTCH DPL BCOND	8	117.1	14.9	<0.001	0.37
AGE GROUP CLUTCH DPL BCOND OWEIGHT GROUP*CLUTCH GROUP*DPL	13	117.6	16.5	<0.001	0.56
GROUP	4	122.7	21.6	<0.001	0.11
AGE GROUP CLUTCH DPL BCOND OWEIGHT GROUP*CLUTCH GROUP*DPL GROUP*AGE	15	124.8	23.7	<0.001	0.57
BCOND	3	125.3	24.2	<0.001	0.01
AGE	3	125.5	24.4	<0.001	0.00

^a Model terms: GROUP = laying groups (captive breeding, wild-trapped, free-ranging hens); CLUTCH = apparent clutch size; DPL = days post-laying at which hens were collected; BCOND = female body condition (adjusted body mass); AGE = female age (second-year or after-second-year); OWEIGHT = ovary weight (± 0.01 g).

^b K = number of parameters used in the model.

^c w_i = Akaike model weight (Burnham and Anderson 1998). Note that values have been rounded up.

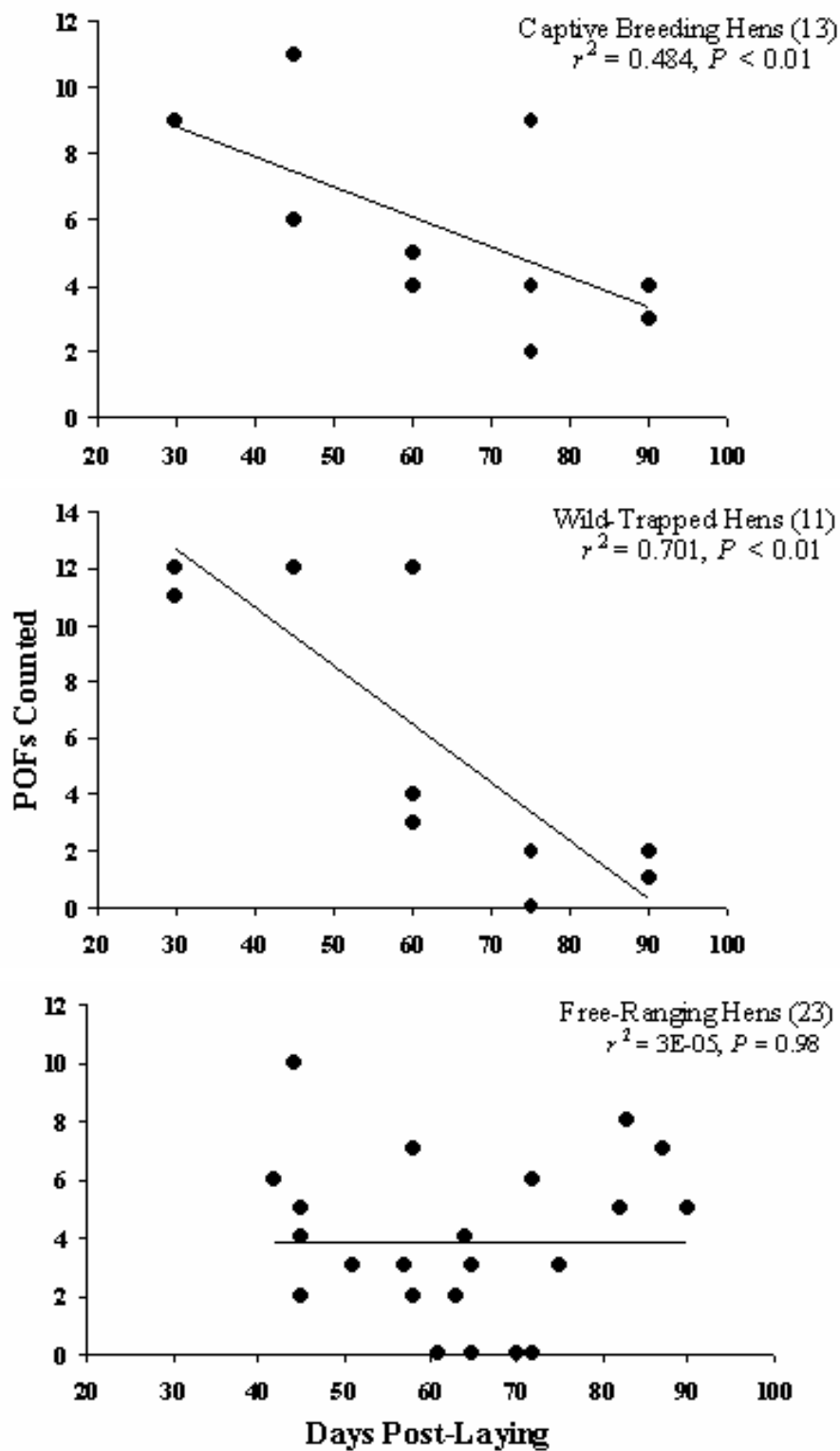


Figure 2.3. The number of postovulatory follicles (POFs) remaining for 47 female mallards collected at 30-90 days post-laying, 2002-03. Sample sizes for each laying group denoted in parentheses.

DISCUSSION

POF AND OVARY REGRESSION

Although several studies have examined POFs in waterfowl (e.g., Wood 1964, Ankney 1974, Krapu 1974, Hamann et al. 1986, Ankney and Afton 1988, Semel and Sherman 1991, Mann and Sedinger 1993, Young 1993, Esler and Grand 1994, Hohman and Crawford 1995, Hohman et al. 1996, Petrie and Rodgers 2004), few have investigated factors that influence POF envelopment rates (but see Esler 1994). Rather, most research has centered on nutrient reserve dynamics of laying or incubating females (Alisauskas and Ankney 1992). To my knowledge, this was the first study to assess individual variation in POF envelopment among female mallards.

I found that POFs (≥ 1) were macroscopically distinguishable in all females collected between 30-60 DPL, and in nearly 80% (19 of 24) of females collected between 61-90 DPL. Only 5 hens (3 WTHs, 1 FRH, and 1 CBH) did not retain visible POFs, and these birds were collected at 61, 65, 70, 71, and 75 DPL. These findings are consistent with Lofts and Murton (1973:45) and Johnson (2000:571) who suggested that POFs can remain discernable up to several months following ovulation in mallards. I also found that the number of POFs remaining differed considerably among individual females. I suspect these differences may have been due to the rapid regression of ovarian follicles that occurred at later post-laying periods. For example, ovary mass declined at increasing DPL, and reached a relatively quiescent (winter) state by approximately 60 DPL (Fig. 2.1.). At this time, POFs may have enveloped beyond recognition in some

hens. Similarly, Johnson (1961) noted that 85-90% of ovary regression occurs within 35 DPL in mallards, and that regression is complete by approximately 53 DPL.

Ovary regression rates also differed among laying groups. Ovaries of WTHs had a significantly larger mass than both CBHs and FRHs after controlling for variation in DPL (Fig. 2.2.). A plausible explanation for these differences may be due to the length of time females incubated their clutch and associated hormone levels. Most CBHs and FRHs incubated their clutch for an entire incubation cycle, whereas, WTHs were captured from their nest during mid-incubation ($\bar{x} = 16.6 \pm 1.9$ SE, range 7-26 DPL). Removing WTHs from their nest during incubation may have simulated a clutch depredation event (i.e., hens were removed from eggs prior to successful hatch). Thus, WTHs may have maintained their ovaries at a breeding state or greater mass for a longer period of time in an attempt to re-nest. Luteinizing hormone (LH) levels will increase dramatically as prolactin secretion decreases following the loss of a clutch in mallards (Bluhm et al. 1983a) and canvasbacks (Bluhm et al. 1983b), thereby causing an increase in follicle size (Campbell et al. 1978).

In contrast, I found no difference in ovary weights between CBHs and FRHs allowed to fully incubate their clutch. These findings suggest that captivity had minimal physiological impacts on ovary regression for hens that fully incubated a clutch. Previous researchers have also suggested that the onset of incubation (i.e., increase in prolactin levels) may accelerate POF regression in American coots (Arnold et al. 1997) and waterfowl (see Bluhm 1992 for review). Thus, differences in ovary regression and POF envelopment rates found in this study could have resulted from variation in hormone

levels. In canvasbacks, LH levels decline 2 days prior to the onset of incubation (Bluhm et al. 1983*b*) and similar trends have been found in mallards (Donham et al. 1976, Bluhm et al. 1983*a*) and snow geese (Campbell et al. 1978). Prolactin levels then increase as female mallards (Bluhm et al. 1983*a*) and canvasbacks (Bluhm et al. 1983*b*) begin to incubate and high prolactin levels are sustained only in females that complete egg laying and become “broody” (Bluhm 1992). Following incubation, prolactin levels decrease more slowly in hens with a brood compared to those hens without (Bluhm 1992). Thus, differences in incubation consistency, brood behavior, and associated hormone levels (e.g., LH and prolactin) may have caused a substantial amount of variation in ovary regression and POF envelopment rates among females.

FACTORS INFLUENCING POF ENVELOPMENT

Johnson (1961) hypothesized that age may influence the degree of ovary hypertrophy and regression in mallards. My findings, however, suggest that the number of POFs remaining did not appear to be strongly influenced by female age.

Environmental factors, such as food availability and habitat conditions, can also have a profound effect on female reproduction and gonad development (Bluhm 1992). For example, arctic nesting geese will reallocate nutrient reserves from their ovaries to meet energetic demands during delayed nesting periods (Ankney 1977, Ankney and MacInnes 1978, Hamann et al. 1986). Therefore, I predicted that hens in better condition would have a greater number of POFs remaining compared to hens in poorer condition. My analysis showed that female body condition had little influence on POF envelopment. I

may have failed to detect an effect of body condition, however, because the vast majority of females appeared to be in good condition relative to other studies. For example, body weights recorded for post-incubating hens in this study were similar or higher than those found for other post-breeding mallards (range 837 - 1,143 grams; Krapu 1981, Gatti 1983). Although body mass and structural size varied among females, I was unable to detect a statistically significant difference in body condition estimates among laying groups (Table 2.1.). These results were somewhat unexpected because both CBHs and WTHs were fed an *ad libitum* diet. Therefore, I would have expected captive females to be in better condition than FRHs due to their high quality diet. These similarities in body condition further suggest that radio-transmitters had minimal adverse effects on FRH condition, and should not have confounded POF envelopment rates.

As predicted, the number of POFs remaining decreased at increasing DPL for most females. These findings are consistent with previous studies that have found that POFs envelop rapidly following ovulation in northern pintail (Krapu 1974, Esler 1994), wood ducks (Semel and Sherman 1991), American wigeon (Esler 1994), and lesser scaup (Esler 1994). I also found that laying group (GROUP) had a significant impact on the number of POFs remaining. Four of the top 6 best approximating models contained the effects of GROUP, DPL, and OWEIGHT. Not surprisingly, my analysis showed that ovary weight was positively correlated to the number of POFs remaining. The most parsimonious model explained a large component of the variation in the data and accounted for a relatively high Akaike weight ($w_i = 0.31$) when compared to other competing models (Table 2.4.). In addition, 4 of the top 6 models all contained the

effects of GROUP suggesting that the number of POFs remaining differed among laying groups.

Further examination of the data revealed that the number of POFs remaining decreased significantly at increasing DPL for both CBHs and WTHs, but not for FRHs (Fig. 2.3.). Again, I suspect that these differences were due to variation in hormonal levels among individuals. The length of time FRHs had a brood (BROODDAYS) did not appear to affect the number of POFs remaining after accounting for variation in DPL. I may have failed to detect a strong influence of brood behavior, however, because these results were based on a small sample of females ($n = 23$). Interestingly, clutch size appeared to have little to no effect on POF envelopment rates. Arnold et al. (1997) noted that large clutch sizes may decrease the ability to distinguish POFs in American coots for a prolonged period of time. Also, females that lay large clutches may invest large amounts of nutrient reserves towards egg production and incubation (Alisauskas and Ankney 1992) and accelerate POF envelopment. If this were true, however, I would have expected female body condition to have a substantial effect on the number of POFs remaining.

In summary, I suspect the variation in POF envelopment observed in this study was due to a number of measured (e.g., DPL, GROUP, OWEIGHT) and unmeasured (day length, temperature, hormones) variables. Clearly, a number of environmental and social factors that could have influenced POF envelopment and photorefractoriness were unaccounted for. Nevertheless, results of this study provide vital information regarding some of the underlying physiological and ecological mechanisms influencing POF

envelopment in mallards. These findings may be particularly useful for future studies that examine POF persistence in other waterfowl species of interest, such as northern pintail and scaup. Continued investigation is needed to fully understand how other factors (e.g., hormone levels, photoperiod length) influence POF envelopment in post-breeding waterfowl. Advancement in these areas will improve our understanding of the various physiological and environmental mechanisms influencing POF envelopment.

LITERATURE CITED

- Afton, A. D. 1984. Influence of age and time on reproductive performance of female lesser scaup. *Auk* 101:255-265.
- _____, and S. L. Paulus. 1992. Incubation and brood care. Pages 62-108 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. *Ecology and management of breeding waterfowl*. University Minnesota Press, Minneapolis, Minnesota, USA.
- Alisauskas, R. T., and C. D. Ankney. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl. Pages 30-61 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. *Ecology and management of breeding waterfowl*. University Minnesota Press, Minneapolis, Minnesota, USA.
- Anderson, M. G., M. S. Lindberg, and R. B. Emery. 2001. Probability of survival and breeding for juvenile female canvasbacks. *Journal of Wildlife Management* 65: 385-397.
- Ankney, C. D. 1974. The importance of nutrient reserves to breeding Blue Geese, *Anser caerulescens*. Dissertation, University of Western Ontario, London, Ontario, Canada.
- _____. 1977. The use of nutrient reserves by breeding male lesser snow geese, *Chen caerulescens caerulescens*. *Canadian Journal of Zoology* 55:1984-1987.
- _____, and A. D. Afton. 1988. Bioenergetics of breeding northern shovelers: diet, nutrient reserves, clutch size, and incubation. *Condor* 90:459-472.
- _____, and C. D. MacInnes. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. *Auk* 95:459-471.
- Arnold, T. W. 1990. Food limitation and the adaptive significance of clutch size in American coots (*Fulica americana*). Dissertation, University of Western Ontario, London, Ontario, Canada.
- Arnold, T. W., J. E. Thompson, and C. D. Ankney. 1997. Using post-ovulatory follicles to determine laying histories of American coots: Implications for nutrient-reserve studies. *Journal of Field Ornithology* 68:19-25.
- Barry, T. W. 1962. Effect of late seasons on Atlantic brant reproduction. *Journal of Wildlife Management* 26:19-26.

- Barzen, J. A. and J. R. Serie. 1990. Nutrient reserve dynamics of breeding canvasbacks. *Auk* 107:75-85.
- Batt, B. D. J., A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec and G. L. Krapu, editors. 1992. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, Minnesota, USA.
- _____, and H. H. Prince. 1978. Some reproductive parameters of mallards in relation to age, captivity, and geographic origin. *Journal of Wildlife Management* 42:834-842.
- _____, and _____. 1979. Laying dates, clutch size and egg weight of captive mallards. *Condor* 81:35-41.
- Bellrose, F. C. 1980. Ducks, geese and swans of North America. Third edition. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Bluhm, C. K. 1992. Environmental and endocrine control of waterfowl reproduction. Pages 323-364 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University Minnesota Press, Minneapolis, Minnesota, USA.
- _____, R. E. Phillips, and W. H. Burke. 1983a. Serum levels of luteinizing hormone, prolactin, estradiol and progesterone in laying and non-laying mallards (*Anas platyrhynchos*). *Biology of Reproduction* 28:295-305.
- _____, R. E. Phillips, and W. H. Burke. 1983b. Serum levels of luteinizing hormone (LH), prolactin, estradiol, and progesterone in laying and non-laying canvasback ducks (*Aythya valisineria*). *General and Comparative Endocrinology* 52:1-16.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Buss, I. O., R. K. Meyer, and C. Kabat. 1951. Wisconsin pheasant reproduction studies based on ovulated follicle technique. *Journal of Wildlife Management* 15:32-46.
- Campbell, R. R., Ashton, S. A., Follett, B. K., and Leatherland, J. F. 1978. Seasonal changes in plasma concentration of LH in the lesser snow goose (*Anser caerulescens caerulescens*). *Biology of Reproduction* 18:663-668.
- Coulter, M. W., and W. R. Miller. 1968. Nesting biology of black ducks and mallards in northern New England Vermont Fish and Game Bulletin 38:2.

- Cowardin, L. M., D. S. Gilmer, and C. W. Shaiffer. 1985. Mallard recruitment in the agricultural environment of North Dakota. *Wildlife Monographs* 92.
- Curson, D. R., and N. E. Mathews. 2003. Reproductive costs of commuting flights in brown-headed cowbirds. *Journal of Wildlife Management* 67:520-529.
- Davis, D. E. 1942*a*. The regression of the avian postovulatory follicle. *Anatomical Record* 82:297-307.
- _____. 1942*b*. The number of eggs laid by cowbirds. *Condor* 44:10-12.
- _____. 1958. Relation of "clutch size" to number of ova ovulated by starlings. *Auk* 75:60-66.
- Dolbeer, R. A., and G. E. Bernhardt. 2003. Age-specific reproduction by female laughing gulls (*Larus atricilla*). *Auk* 120:532-535.
- Donham, R. S., C. W. Dane, and D. S. Farner. 1976. Plasma luteinizing hormone and the development of ovarian follicles after loss of clutch in female mallards (*Anas platyrhynchos*). *General and Comparative Endocrinology* 29:152-155.
- Drilling, N., R. Titman, and F. McKinney. 2002. Mallard (*Anas platyrhynchos*). in A. Poole and F. Gill, editors. *The Birds of North America*, No. 658. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.
- Dufour, K. W., C. D. Ankney, and P. J. Weatherhead. 1993. Condition and vulnerability to hunting among mallards staging at Lake St. Clair, Ontario. *Journal of Wildlife Management* 57:209-215.
- Dwyer, T. J. 1972. An adjustable radio-package for ducks. *Bird Banding* 43:282-284.
- Earle, J. P. 1950. Production of mallards on irrigated land in the Sacramento Valley, California. *Journal of Wildlife Management* 14:332-342.
- Eldridge, J. L. and G. L. Krapu. 1988. The influence of diet quality on clutch size and laying pattern in mallards. *Auk* 105:102-110.
- Erpino, M. J. 1969. Seasonal cycle of reproductive physiology in the black-billed Magpie. *Condor* 71:267-279.
- Esler, D. 1994. Dynamics of ovarian follicles in breeding ducks. *Wilson Bulletin* 106:679-688.

- _____, and J. B. Grand. 1994. The role of nutrient reserves for clutch formation by female northern pintails in subarctic Alaska. *Condor* 96:422-432.
- Gatti, R. C. 1983. Incubation weight loss in the mallard. *Canadian Journal of Zoology* 61:565-569.
- Gilmer, D. S., I. J. Ball, L. M. Cowardin, and J. H. Reichmann. 1974. Effects of radio packages on wild ducks. *Journal of Wildlife Management* 38:243-252.
- _____, L. M. Cowardin, R. L. Duval, L. M. Mechlin, C. W. Shaffer, and V. B. Kuechle. 1981. Procedures for the use of aircraft in wildlife biotelemetry studies. U. S. Fish and Wildlife Resource Publication No. 140.
- _____, M. R. Miller, R. D. Bauer, and J. R. LeDonne. 1982. California's Central Valley wintering waterfowl: concerns and challenges. *Transactions of the North American Wildlife and Natural Resources Conference* 47:441-452.
- Gloutney, M. L., R. G. Clark, A. D. Afton, and G. J. Huff. 1993. Timing of nest searches for upland nesting waterfowl. *Journal of Wildlife Management* 57:597-601.
- Greenwood, R. J., A. B. Sargeant, D. H. Johnson, L. M. Cowardin, and T. L. Schaffer. 1995. Factors associated with nest success in the prairie pothole region of Canada. *Wildlife Monographs* 128.
- Grinnell, J., H. C. Bryant, and T. I. Storer. 1918. *The game birds of California*. University of California Press, Berkeley, California, USA.
- Hamann, J., B. Andrews, and F. Cooke. 1986. The role of follicular atresia in inter- and intra-seasonal clutch size variation in Lesser Snow Geese (*Anser caerulescens caerulescens*). *Journal of Animal Ecology* 55:481-489.
- Hannon, S. J. 1981. Postovulatory follicles as indicators of egg production in blue grouse. *Journal of Wildlife Management* 45:1045-1047.
- Hansen, H. A. and D. E. McKnight. 1964. Emigration of drought-displaced ducks to the arctic. *Transactions of the North American Wildlife and Natural Resources Conference* 29:119-127.
- Heitmeyer, M. E., D. P. Connelly, and R. L. Pederson. 1989. The Central, Imperial and Coachella Valleys of California. Pages 475-505 *in* L. M. Smith, R. L. Pederson, and R. M. Kaminski, editors. *Habitat management for migrating and wintering waterfowl in North America*. Texas Tech University Press, Lubbock, Texas, USA.

- Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Deveries, and I. J. Ball. 2002. Sensitivity analysis of the mid-continent mallard life cycle. *Journal of Wildlife Management* 66:883-901.
- Hohman, W. L., and R. D. Crawford. 1995. Molt in the annual cycle of ring-necked ducks. *Condor* 97:473-483.
- _____, T. M. Stark, and J. L. Moore. 1996. Food availability and feeding preferences of breeding fulvous whistling-ducks in Louisiana ricefields. *Wilson Bulletin* 108:137-150.
- Jenner, E. 1788. Observations on the natural history of the Cuckoo. *Philosophical Transactions of the Royal Society London* 78:237-246.
- Johnsgard, P. A. 1978. Ducks, geese, and swans of the world. University of Nebraska Press, Lincoln, Nebraska, USA.
- Johnson, A. L. 2000. Reproduction in the female. Pages 569-596. *in* G. C. Whittow, editor. *Sturkie's avian physiology*. Fifth edition. Academic Press, San Diego, California, USA.
- Johnson, O. W. 1961. Reproductive cycle of the mallard duck. *Condor* 63:351-364.
- Johnson, D. H., and J. W. Grier. 1988. Determinants of breeding distributions of ducks. *Wildlife Monographs* 100:1-37.
- _____, J. D. Nichols, and M. D. Schwartz. 1992. Population dynamics of breeding waterfowl. Pages 446-485 *in* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec and G. L. Krapu, editors. *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Jull, M. A. 1934. Egg weight in relation to production. *Poultry Science* 3:77-88.
- Kabat, C., I. O. Buss, and R. K. Meyer. 1948. The use of ovulated follicles in determining eggs laid by the ring-necked pheasant. *Journal of Wildlife Management* 12:399-416.
- Kendall, W. L., and J. D. Nichols. 1995. On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportions. *Journal of Applied Statistics* 22:751-762

- Kennedy, E. D., P. C. Stouffer, and H. W. Power. 1989. Postovulatory follicles as a measure of clutch size and brood parasitism in European Starlings. *Condor* 91:471-473.
- Klett, A. T., H. F. Duebbert, C. A. Faanes, and K. F. Higgins. 1986. Techniques for studying nest success of ducks in upland habitats in the prairie pothole region. U.S. Fish and Wildlife Service Resource Publication No. 158.
- Krapu, G. L. 1974. Feeding ecology of pintail hens during reproduction. *Auk* 91:278-290.
- _____. 1981. The role of nutrient reserves in mallard reproduction. *Auk* 98:29-38.
- _____. 2000. Temporal flexibility of reproduction in temperate-breeding dabbling ducks. *Auk* 177:640-650.
- _____, D. H. Johnson, and C. W. Dane. 1979. Age determination of mallards. *Journal of Wildlife Management* 42:384-393.
- _____, A. T. Klett and D. G. Jorde. 1983. The effect of variable spring water conditions on mallard reproduction. *Auk* 100:689-698.
- Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press, London, England.
- Laurila, T. 1988. Reproductive strategies in waterfowl: the effect of ultimate environmental factors, size, and phylogeny. *Ornis Fennica* 65:49-64.
- Lebreton, J.-D., G. Henry, J. Clobert, and H. Coquillart. 1990. The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrate populations. I. Transversal models. *Biometrics* 46:609-622.
- Lewin, V. 1963. Reproduction and development of young in a population of California quail. *Condor* 65:249-278.
- Lofts, B., and R. K. Murton. 1973. Reproduction in birds. Pages 1-107 in D. S. Farner, J. R. King, and K. C. Parkes, editors. *Avian Biology*, Volume 3. Academic Press, New York, New York, USA.
- Lokemoen, J. T., and D. E. Sharp 1985. Assessment of nasal marker materials and designs used on dabbling ducks. *Wildlife Society Bulletin* 13:53-56.

- _____, D. H. Johnson, and D. E. Sharp. 1990. Weights of wild mallard *Anas platyrhynchos*, gadwall *A. strepera*, and blue-winged teal *A. discors* during the breeding season. *Wildfowl* 41:122-130.
- Loughman, D., J. Laughlin, and E. Burns. 2004. Evaluating the Conservation Reserve Enhancement Program in California. Final Report for the California Department of Fish and Game No. P0180089.
- MacInnes, C. D., and E. H. Dunn. 1988. Estimating proportion of age class nesting in Canada Geese. *Condor* 90:83-89.
- Mann, F. E., and J. S. Sedinger. 1993. Nutrient-reserve dynamics and control of clutch size in northern pintails breeding in Alaska. *Auk* 110:264-278.
- Mayhew, W. W. 1955. Spring rainfall in relation to mallard production in the Sacramento Valley, California. *Journal of Wildlife Management* 19:36-47.
- McKinney, F. 1992. Courtship, pair formation, and signal systems. Pages 214-250 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. *Ecology and management of breeding waterfowl*. University Minnesota Press, Minneapolis, Minnesota, USA.
- McLandress, M. R., G. S. Yarris, A. E. H. Perkins, D. P. Connely, and D. G. Raveling. 1996. Nesting biology of California mallards. *Journal of Wildlife Management* 60:94-107.
- Meyer, R. K., C. Kabat, and I. O. Buss. 1947. Early involutary changes in post-ovulatory follicles of the ring-necked pheasant. *Journal of Wildlife Management* 11:43-49.
- Mills, L. S., and M. S. Lindberg. 2002. Sensitivity analysis to evaluate the consequences of conservation actions. Pages 338-366 in S. R. Beissinger and D. R. McCullough, editors. *Population Viability Analysis*. University of Chicago Press, Chicago, Illinois, USA.
- Newton, I. 1988. Age and reproduction in the Sparrowhawk. Pages 201-219 in T. H. Clutton-Brock, editor. *Reproductive Success*. University of Chicago Press, Chicago, Illinois, USA.
- Paquette, G. A., J. H. Devries, R. B. Emery, D. W. Howerter, B. L. Joynt, and T. P. Sankowski. 1997. Effects of transmitters on reproduction and survival of wild mallards. *Journal of Wildlife Management* 61:953-961.

- Payne, R. B. 1965. Clutch size and numbers of eggs laid by brown-headed cowbirds. *Condor* 44-60.
- _____. 1966. The postovulatory follicles of blackbirds (*Agelaius*). *Journal of Morphology* 118:331-352.
- _____. 1973. Individual laying histories and the clutch size and numbers of eggs of parasitic cuckoos. *Condor* 75:414-438.
- Pearson, S. F., and S. Rohwer. 1998. Determining clutch size and laying dates using ovarian follicles. *Journal of Field Ornithology* 69:587-594.
- Pehrsson, O. 1991. Egg and clutch size in the mallard as related to food quality. *Canadian Journal of Zoology* 69:156-162.
- Petrie, S. A., and K. H. Rodgers. 2004. Nutrient reserve dynamics of semiarid-breeding white-faced whistling ducks: a north-temperate contrast. *Canadian Journal of Zoology* 82:1082-1090.
- Phillips, R. E. 1936. Observations on the mechanisms of ovulation in the fowl. *Poultry Science* 15:413.
- Pietz, P. J., G. L. Krapu, R. J. Greenwood, and J. T. Lokemoen. 1993. Effects of harness transmitters on behavior and reproduction of wild mallards. *Journal of Wildlife Management* 57:696-703.
- Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:757-760.
- Pospahala, R. S., D. R. Anderson and C. J. Henny. 1974. Population ecology of the mallard: II. Breeding habitat conditions, size of breeding populations and production indices. U.S. Fish and Wildlife Service Resource Publication No. 115.
- Raveling, D. G. 1979. The annual cycle of body composition of Canada geese with special reference to control of reproduction. *Auk* 96:234-252.
- Rhymer, J. M. 1988. Experimental study of geographical variation in reproductive and developmental traits of mallard ducks. Dissertation, Florida State University, Tallahassee, Florida, USA.
- Robb, J. R. 2002. Band recovery and recapture rates of American black ducks and mallards. *Journal of Wildlife Management* 66:153-161.

- Rohwer, F. C. 1992. The evolution of reproductive patterns in waterfowl. Pages 486-539 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press. Minneapolis, Minnesota, USA.
- Rotella, J. J., D. W. Howerter, T. P. Sankowski, and J. H. Devries. 1993. Nesting effort by mallards with 3 types of radio transmitters. *Journal of Wildlife Management* 57:690-695.
- SAS Institute. 1999. SAS online document. Version 8. SAS Institute, Cary, North Carolina, USA.
- Scott, D. M., and C. D. Ankney 1983. The laying cycle of brown-headed cowbirds: passerine chickens? *Auk* 100:583-592.
- Scott, H. M., and D. C. Warren. 1936. Influence of ovulation rates on the tendency of fowl to produce eggs in clutches. *Poultry Science* 15:381-389.
- Sedinger, J. S., M. S. Lindberg, and N. D. Chelgren. 2001. Age-specific breeding probability in black brant: effects of population density. *Journal of Animal Ecology* 70:798-807.
- Semel, B., and P. Sherman. 1991. Ovarian follicles do not reveal laying histories of post-incubation wood ducks. *Wilson Bulletin* 103:703-705.
- Sheaffer, S. and R. A. Malecki. 1999. Models for adaptive harvest management of western mallards. Final Report Pacific Flyway Study Committee, Sacramento, California, USA.
- Sokal, R. R., and F. J. Rohlf. 2000. *Biometry*. Third edition. W. H. Freeman and Company, New York, New York, USA.
- Sowls, L. K. 1955. *Prairie ducks. A study of their behavior, ecology, and management*. Stackpole Co., Harrisburg, Pennsylvania and Wildlife Management Institute, Washington, D.C., USA.
- Standing, K. M. 1960. Factors in relation to population fluctuations in the blue grouse. Dissertation, Washington State University, Pullman, Washington, USA.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, New York, New York, USA.

- Trost, R. E. and M. S. Drut. 2003. Pacific Flyway Data Book: waterfowl harvests and status, hunter participation and success, and certain hunting regulations in the Pacific Flyway and United States. U.S. Fish and Wildlife Service, Division of Migratory Bird Management, Portland, Oregon, USA.
- U.S. Prairie Pothole Joint Venture. 1995. U.S. Prairie Pothole Joint Venture Implementation Plan (update). 86pp.
- Viallefont, A., F. Cooke, and J.-D. Lebreton. 1995. Age-specific costs in first time breeding. *Auk* 112:67-76.
- Ward, P., and B. D. J. Batt. 1973. Propagation of captive waterfowl. Wildlife Management Institute, Washington, D.C., USA.
- Weller, M. W. 1956. A simple field candler for waterfowl eggs. *Journal of Wildlife Management* 20:111-113.
- _____. 1957. An automatic nest-trap for waterfowl. *Journal of Wildlife Management* 21:456-458.
- Williams, B. K., and J. D. Nichols. 1990. Modeling and management of migratory birds. *Natural Resource Modeling* 4:273-311.
- Wisdom, M. J., L. S. Mills, and D. F. Doak. 2000. Life-stage simulation analysis: estimating vital-rate effects on population growth for conservation. *Ecology* 81:628-641.
- Wood, J. S. 1964. Normal development and causes of reproduction failure in Canada geese. *Journal of Wildlife Management* 28:197-208.
- Yarris, G. S., M. R. McLandress, and A. E. H. Perkins. 1994. Molt migration of postbreeding female mallards from Suisun Marsh, California. *Condor* 96:36-45.
- Yerkes, Tina. 1997. A trap for ducks using artificial nesting structures. *Journal of Field Ornithology* 68:147-149.
- Young, A. D. 1993. Intraspecific variation in the use of nutrient reserves by breeding female mallards. *Condor* 95:45-56.

APPENDICES

Appendix A. Total number of eggs laid and hatching success for 42 nesting mallard hens radio-marked in Colusa and Yolo Counties, California, 2003.

Study Site	n^a	Successful Nests	Laid	Hatched	Hatch Success ^b
Ottenwalter Wheat	25	20	227	143	0.63
Fendt	11	9	109	63	0.58
Newman	4	2	43	18	0.42
Kalfsbeck ^c	2	2	18	15	0.83
Total	42	33	397	239	0.60

^adenotes number of hens radio-marked at each study site.

^bcalculated as # of eggs successfully hatched divided by the total # of eggs laid.

^cKalfsbeck North and South data combined.

Appendix B. Postovulatory follicle (POF) counts recorded during macroscopic examination of 48 mallard ovaries collected at 30-90 days following the completion of egg laying, 2002-03.

Hen	Laying Group ^a	Days Post-laying	POFs Counted	Apparent Clutch Size	POF:Clutch Ratio	Difference (+/-) ^c
3808	CBH	30	9	9	1.00	--
3812	CBH	30	9	14	0.64	-5
019	WTH	30	12	11	1.09	+1
021	WTH	30	11	6	1.83	+5
172.571	FRH	34	12	12	1.00	--
172.851	FRH	42	6	9	0.67	-3
172.689	FRH	44	10	10	1.00	--
3811	CBH	45	11	10	1.10	+1
3801	CBH	45	6	7	0.86	-1
013	WTH	45	12	10	1.20	+2
018	WTH	45	12	12	1.00	--
172.631	FRH	45	4	10	0.40	-6
172.280	FRH	45	5	9	0.56	-4
Noradio	FRH	45	2	9	0.22	-7
172.808	FRH	51	3	9	0.33	-6
172.910	FRH	57	3	11	0.27	-8
172.239	FRH	58	7	9	0.78	-2
172.613	FRH	58	2	10	0.20	-8

Appendix B. Continued.

Hen	Laying Group ^a	Days Post-laying	POFs Counted	Apparent Clutch Size	POF:Clutch Ratio ^b	Difference (+/-) ^c
3173	CBH	60	5	8	0.63	-3
3807	CBH	60	5	7	0.71	-2
3184	CBH	60	4	7	0.57	-3
015	WTH	60	12	10	1.20	+2
022	WTH	60	4	5	0.80	-1
023	WTH	60	3	9	0.33	-6
172.472	FRH	61	0	10	0.00	-10
172.413	FRH	63	2	8	0.25	-6
172.710	FRH	64	4	8	0.50	-4
172.902	FRH	65	0	8	0.00	-8
172.423	FRH	65	3	10	0.30	-7
172.771	FRH	70	0	8	0.00	-8
172.841	FRH	72	0	10	0.00	-10
172.092	FRH	72	6	9	0.67	-3
3380	CBH	75	4	10	0.40	-6
3387	CBH	75	2	10	0.20	-8
3593	CBH	75	9	10	0.90	-1
017	WTH	75	2	9	0.22	-7
020	WTH	75	0	12	0.00	-12

Appendix B. Continued.

Hen	Laying Group ^a	Days Post-laying	POFs Counted	Apparent Clutch Size	POF:Clutch Ratio ^b	Difference (+/-) ^c
172.363	FRH	75	3	10	0.30	-7
172.621	FRH	75	3	10	0.30	-7
172.017	FRH	82	5	4	1.25	+1
172.640	FRH	83	8	14	0.57	-6
172.720	FRH	87	7	9	0.78	-2
3392	CBH	90	4	9	0.44	-5
3197	CBH	90	3	9	0.33	-6
2553	CBH	90	4	6	0.67	-2
014	WTH	90	1	9	0.11	-8
016	WTH	90	2	11	0.18	-9
172.253	FRH	90	5	11	0.45	-6

^aCBH = Captive-breeding hen, WTH = Wild-trapped hen, FRH = Free-ranging hen.

^bCalculated as (number of POFs counted/apparent clutch size).

^cPositive (+) integers = overestimation, negative (-) integers = underestimation, and dashed line (-) = perfect concordance.

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