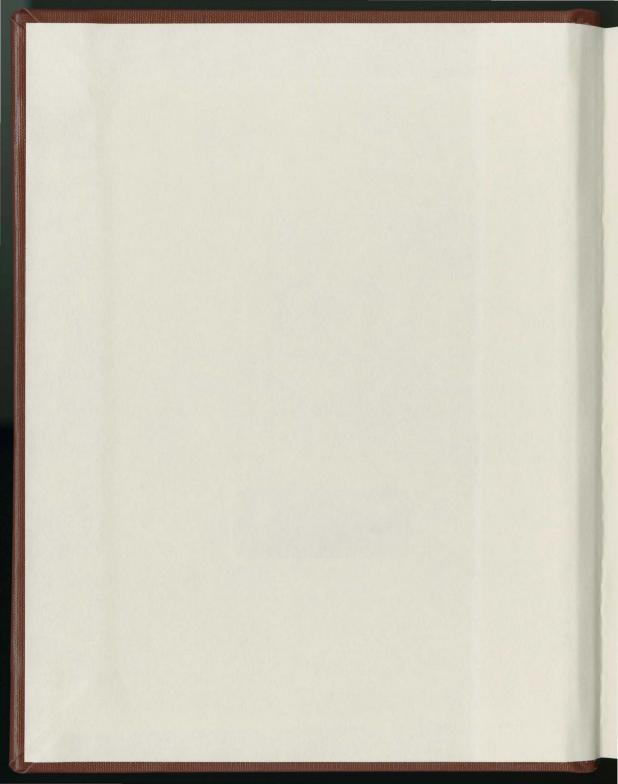
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THESIS

EVALUATING GREATER SAGE-GROUSE BROOD HABITAT USING HUMAN-IMPRINTED CHICKS

Submitted by

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In partial fulfillment of the requirements

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY SHERRI LYNN HUWER ENTITLED "EVALUATING GREATER SAGE-GROUSE BROOD HABITAT USING HUMAN-IMPRINTED CHICKS" BE ACCEPTED AS FULLFILING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

EVALUATING GREATER SAGE-GROUSE BROOD HABITAT USING HUMAN-IMPRINTED CHICKS

Greater sage-grouse (Centrocercus urophasianus) populations are experiencing longterm declines throughout their current range. Several researchers have suggested that the quality and availability of brood habitat may be limiting populations through reductions in the recruitment of young. In order to effectively manage brood areas, reliable information is needed on chick resource requirements and the role of various components of the habitat in chick growth, development and survival. Forb abundance has been identified by several studies as an indicator of brood habitat quality, but no studies have quantified the direct effects of forb abundance on sage-grouse chicks. A promising method for conducting such studies involves using humanimprinted sage-grouse chicks in field experiments. In 2002 and 2003, I conducted field experiments in Middle Park and Moffat County, Colorado, respectively. The objectives of these studies were (1) to develop and evaluate methods for acquiring human-imprinted sage-grouse chicks and using them in field experiments; and (2) to quantify the effects of 3 levels of forb abundance (i.e., < 10%, 10 - 20%, and > 20%) in brood habitat on the growth of these chicks. The egg acquisition, incubation, imprinting, and field exposure methods used resulted in humanimprinted sage-grouse chicks that were successfully used in field experiments. These studies showed that using human-imprinted sage-grouse chicks in field experiments is, potentially, a very informative approach to investigating a variety of grouse-habitat relationships. In 2002, there was no evidence that forb abundance in the exposure areas had an effect on the rate of mass gain or feather growth. However, in 2003, the mass gain and feather growth rate of chicks increased

with increasing forb abundance. Previous studies have shown a correlation between chick mass and long-term survival. Management actions that increase forb abundance in brood areas with < 20% forb abundance may, therefore, lead to increased chick survival and sage-grouse productivity.

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INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*) populations are experiencing long-term declines throughout the current range of the species (Connelly and Braun 1997). Concern over these population declines has led to conservation efforts at regional, state, and local levels. Several authors have suggested that the quality and availability of brood habitat may be limiting populations through reductions in the recruitment of young (Drut et al. 1994*a*, *b*; Connelly and Braun 1997; Sveum et al. 1998). Previous studies have indicated that forbs are an important resource for chicks by showing correlations between forb abundance in brood habitat and brood success (Autenrieth 1981), and productivity (Drut et al. 1994*b*). Similarly, studies have suggested that forbs play a role in brood habitat selection (Klebenow 1969, Wallestad 1971, Drut et al. 1994*a*, Sveum et al. 1998), brood movements (Klebenow 1969, Wallestad 1971, Autenrieth 1981), brood distribution (Peterson 1970, Wallestad 1971), and home range size (Drut et al. 1994*a*).

The most commonly proposed mechanism behind these relationships is the influence that forbs have on the ability of the habitat to fulfill the chicks' nutritional requirements. Several studies have shown that the diet of wild sage-grouse chicks is dominated by forbs and invertebrates for the first 12 weeks of life (Klebenow and Gary 1968, Peterson 1970). In laboratory studies, Johnson and Boyce (1990) have shown that chick growth and survival rates increases with the quantity of invertebrates in the diet and that invertebrates forage is required for survival until chicks are at least 21-days old. Similarly, Jorgensen and Blix (1985) found that both growth and survival rates of captive willow ptarmigan (*Lagopus lagopus*) chicks increased with the protein concentration of their food. Savory (1989) reported that high protein

concentrations are required by young sage-grouse chicks in order to develop the flight muscles and feathers needed for flight. Forbs contribute to the protein intake of chicks directly as food items and, more importantly, indirectly by attracting the invertebrates required for survival and growth (Blenden 1986, Brush 1986).

Although several studies have suggested that forbs in brood habitats may influence chick movements, growth, and survival, no studies have directly quantified the effects of forb abundance in brood areas on sage-grouse chicks. In order to effectively manage brood areas, reliable information is needed on chick resource requirements and the role of various resources in chick growth, development and survival. Experimental studies are, therefore, needed to quantify effects, determine cause-effect relationships, identify the mechanisms behind observed relationships, and reduce the possibility of spurious results due to confounding variables (Romesburg 1981). The ability to conduct field experiments with wild sage-grouse is, however, limited by the difficulty of (1) monitoring wild birds without influencing the response variables of interest; and (2) attaining adequate sample sizes within a manageable study area given the large spatial scales on which sage-grouse operate and due to their low densities during most of the year. Captive studies are limited by the difficulty of (1) maintaining and propagating sage-grouse in captivity; and (2) applying laboratory results to field situations.

In order to overcome the limitations of field experiments on wild birds and of laboratory experiments on captive birds, studies have been conducted using human-imprinted birds exposed to field conditions. Such studies have been performed with several species including turkeys (Meleagris gallopavo, Healy 1978), gray partridge (Perdix perdix, Erpelding et al. 1987), ringnecked pheasant (Phasianus colchicus, Kimmel 1985), ruffed grouse (Bonasa umbellus, Kimmel and Samuel 1978, Sharpe et al. 1998), bobwhite quail (Colinus virginianus, Palmer et al. 2001) and ducks (Anas rubripes, A. platyrhynchos, and Aix sponsa; Hunter et al. 1985). These studies have taken advantage of the imprinting process, through which a newly hatched chick forms a social attachment with the hen (Hess 1973). After imprinting, the chicks respond to the

researcher approximately as they would to the hen and behave normally in the presence of the researcher. Assuming that the behavior of greater sage-grouse is innate and not substantially affected by imprinting on humans, a wide range of grouse-habitat relationships could be studied by exposing human-imprinted grouse to field conditions. Such studies would allow researchers to monitor response variables without influencing them, control the size and location study area and control sample size. In addition, the results of such studies could be more reliably applied to the field situation than the results of studies conducted in the laboratory.

In 2002 and 2003, I conducted field experiments in Middle Park and Moffat County, Colorado, respectively. The objectives of these studies were (1) to develop and evaluate methods for acquiring human-imprinted sage-grouse chicks and exposing them to field conditions; and (2) to quantify the effects of 3 levels of forb abundance (i.e., < 10%, 10 - 20%, and > 20%) in brood habitat on the growth of these chicks. In Chapter 2 of this thesis, I describe and evaluate the methods used to acquire human-imprinted sage-grouse chicks and expose them to field conditions. I also discuss possible applications of this method in studies of grouse-habitat interactions. In Chapter 3, I describe and present the results of studies conducted to evaluate the effects of forb abundance in brood areas on the growth of sage-grouse chicks. I then identify future research needs and management implications.

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ACQUISITION AND USE OF HUMAN-IMPRINTED SAGE-GROUSE FOR FIELD STUDIES

ABSTRACT

Greater sage-grouse (Centrocercus urophasianus) populations are experiencing longterm declines throughout their current range. Several authors have suggested that the quality and availability of brood habitat may be limiting populations through reductions in the recruitment of young. In order to effectively manage brood areas, reliable information is needed on chick resource requirements and the role of various components of the habitat in chick growth, development and survival. A promising method for gathering this information uses humanimprinted sage-grouse chicks in field experiments. The main advantage of this method is that, unlike in studies with wild chicks, the researcher can control the location and movements of the study subjects. It is, therefore, possible to ensure adequate sample sizes and to spatially restrict the study to locations of interest. In addition, the researcher can closely monitor the development and behavior of the chicks without disturbing them. In 2002 and 2003, I conducted field experiments in Middle Park and Moffat County, Colorado, respectively, with the objective of developing and evaluating methods for acquiring human-imprinted sage-grouse chicks and using them in field experiments. The egg acquisition, incubation and imprinting methods used resulted in human-imprinted sage-grouse chicks that were successfully exposed to field conditions. These studies showed that this method is potentially a very informative approach to investigating a variety of grouse-habitat interactions.

INTRODUCTION

Greater sage-grouse (Centrocercus urophasianus) populations are experiencing longterm declines throughout the current range of the species (Connelly and Braun 1997). Concern over these population declines has led to conservation efforts at regional, state, and local levels. Several authors have suggested that the quality and availability of brood habitat may be limiting populations through reductions in the recruitment of young (Drut et al. 1994 a and b, Connelly and Braun 1997, Sveum et al. 1998). In order to effectively manage brood areas, reliable information is needed on chick resource requirements and the role of various resources in chick growth, development and survival. Experimental studies are, therefore, needed to quantify effects, determine cause-effect relationships, identify the mechanisms behind observed relationships, and reduce the possibility of spurious results due to confounding variables (Romesburg 1981). The ability to conduct field experiments with wild sage-grouse, however, is limited by the difficulty of (1) monitoring wild birds without influencing the response variables of interest; and (2) attaining adequate sample sizes within a manageable study area given the large spatial scales on which sage-grouse operate and their low densities during most of the year. Captive studies are limited by the difficulty of (1) maintaining and propagating sage-grouse in captivity; and (2) applying laboratory results to field situations.

In order to overcome the limitations of field experiments on wild birds and of laboratory experiments on captive birds, studies have been conducted using human-imprinted birds exposed to field conditions. Such studies have been performed with various species including turkeys (*Meleagris gallopavo*, Healy 1978), gray partridge (*Perdix perdix*, Erpelding et al. 1987), ringnecked pheasant (*Phasianus colchicus*, Kimmel 1985), ruffed grouse (*Bonasa umbellus*, Kimmel and Samuel 1978, Sharpe et al. 1998), bobwhite quail (*Colinus virginianus*, Palmer et al. 2001) and ducks (*Anas rubripes*, *A. platyrhynchos*, and *Aix sponsa*; Hunter et al. 1985). These studies have taken advantage of the imprinting process, through which a newly hatched chick forms a social attachment with the hen (Hess 1973). After imprinting, the chicks respond to the

researcher approximately as they would to the hen. Assuming that the behavior of greater sage-grouse is innate and not substantially affected by imprinting on humans, grouse-habitat relationships can be studied by exposing human-imprinted grouse to field conditions. Such studies would allow researchers to monitor response variables without influencing them, control the size and location study area and control sample size. In addition, the results of such studies could be more directly applied to the field situation than the results of studies conducted in the laboratory.

In 2002 and 2003, I conducted field experiments in Middle Park and Moffat County, Colorado, respectively, with the objective of developing and evaluating methods for acquiring human-imprinted sage-grouse chicks and using them in field experiments. This was done as part of a study on the importance of forbs in brood habitat to sage-grouse chicks (see Chapter 3). In this chapter, I describe and evaluate the egg acquisition, incubation, imprinting and field exposure techniques used. I then identify additional applications for these techniques.

METHODS

Egg Acquisition

Protocols for the use of sage-grouse in this study were approved by the Colorado State University (02-023A-01) and the Colorado Division of Wildlife Animal Care and Use Committees.

In order to remove chick age as a confounding factor in this study, all of the study chicks were of approximately the same age. Equal-aged chicks were acquired by collecting eggs prior to incubation, storing them until the desired number had been collected and then placing them all in the incubator at the same time. The eggs were collected from the nests of radio-collared hens. During the nesting season, the position of each hen was determined in the morning between 0800 and 1100 by circling her at a radius of approximately 15 feet. The position was recorded using a global positioning system, the hen was left undisturbed, and the site was searched later in the day

to determine if a nest was present. This procedure was repeated until a nest was found, at which time the sage-grouse eggs were removed and replaced with brown chicken eggs that had been sterilized by soaking them in alcohol. This replacement protected the sage-grouse eggs from depredation in a way that did not cause the hen to abandon the nest. The nest was then revisited every 1 to 2 days to collect the newly laid sage-grouse eggs and replace them with chicken eggs. Nest searching and egg collection were conducted during the afternoon in order to minimize disturbance to the hens. After the required number of eggs had been collected, all of the eggs from each of the nests were removed to simulate nest depredation. This was done so that the hens would abandon the nests and possibly establish a new one, thereby reducing the net number of eggs removed from the population. The hens were then monitored to determine if they had renested.

Egg Storage and Incubation

Each collected egg was individually marked, weighed and measured (Appendix). The nest from which it came was recorded and it was stored at 10 to 15 °C and turned once a day (Harvey 1993). In 2002, the eggs were placed into the incubator as soon as the required number of eggs had been collected. In 2003, the eggs were stored long enough to synchronize their hatch with that of the wild chicks in the study area.

The eggs were incubated in a cabinet incubator (Georgia Quail Farm (GQF) Sportsman 1202) equipped with an automatic egg turner, humidity system, and clear acrylic door. During the first 24 days of incubation, the eggs were kept at 37.5 °C and 58% relative humidity. The eggs were automatically turned every 4 hours by rotation of the egg trays, in which the eggs were held. The eggs were weighed and candled approximately every 5 days from Day 7 to Day 23 of incubation in order to monitor mass loss and development. Small adjustments in the humidity were made in order to achieve a 15% egg-mass loss from placement in the incubator to internal pip (Harvey 1993). On the 23rd day of incubation, the eggs were transferred to individual

hatching trays and turning was discontinued. During the remaining days of incubation, the temperature was dropped to 37.2 °C and the relative humidity increased to 80%.

Evidence for relationships between hatchability and 4 factors (i.e., egg volume, egg mass at collection, egg density, and storage duration) were sought using an information-theoretic approach (Burnham and Anderson 2002). In this analysis, the hatch data from 2002 and 2003 were pooled and 4 logistic regression models were formulated each representing the hypothesis that 1 of the above factors affected hatchability. The Akaike Information Criteria corrected for small sample size (AIC_C) value of each of these models was compared to that of a model representing the hypothesis that the factor had no effect on hatchability. Egg volume was calculated as the length * width² * 0.51 (Harvey 1993).

Imprinting and Training

Imprinting proceeded according to Healy (1978, see also Healy and Goetz 1974 for figures). Each chick was removed from the incubator within minutes of completely freeing itself from the shell. It was then individually marked with a numbered leg band and held in the jacket pocket of an observer until it was dry, at which time it was weighed and placed into the imprinting ring. The imprinting ring consisted of a 2.5-m diameter, 0.3-m high, cardboard barrier placed on a bed sheet on the floor. An observer sat inside the ring on a heating pad. The chicks were initially placed on the heating pad, but were allowed to explore the imprinting ring, returning to the observer for warmth when necessary. The chicks remained in this ring through Day 2 (Day 0 was defined as the mean hatch day). An observer was present in the ring 24 hours a day during this time. Food and water were present in the ring. The food consisted of mealworms, approximately 1.5 cm long (Rainbow mealworms, Inc.), chopped hardboiled egg, spinach, collard greens and carrots. More than 1 observer was present during most of the hatching and imprinting. Observers talked to each other and to the chicks to expose the chicks to the human voice throughout the hatching and imprinting processes.

In 2002 the chicks remained indoors during imprinting. In 2003, the imprinting ring was moved outside during the afternoon of Day 0 to expose chicks to sagebrush habitat while restraining their movements. In both years, the chicks were taken to 1 of the study sites during the afternoon of Day 1 and released to feed.

During the afternoon of Day 0, the chicks were taught to use portable brooders for thermoregulation. Each brooder consisted of a 32-L cooler with a built-in heating unit and thermostat, powered by either an AC or DC electrical source (Dean's Animal Supply, Inc., Orlando, FL) (Fig. 1.1). A piece of cloth was placed on the floor of each brooder. The lid was made of Perspex. An additional foam lid was added to increase heat retention and a 10-by-10-cm hinged door was added to 1 of the corners of each brooder. The brooders were laid on their sides with the doors positioned to allow the chicks to enter and exit freely. The observers sat on top of the brooders and encouraged the chicks to enter when they returned to the observers for warmth.

Mullin (1978) recommended initially brooding game bird chicks at 35 °C degrees and then decreasing the temperature by 2.8 to 4 °C a week depending on the behavior of the chicks (i.e., huddling near the heat source indicates the brooder is too cool, spreading out and panting indicates the brooder is too hot). Following this guideline, the brooders in this study were initially set at 35 °C. At this temperature, the chicks huddled in the corner nearest the heating element indicating the brooder was too cool. The temperature was, therefore, increased to 36.7 °C. The temperature was then decrease on average 2.8 °C per week until the brooders were set at 31.1 °C (2 weeks). This temperature was then maintained for the rest of the study.

Field Exposures

The human-imprinted chicks acquired by the methods described above were used in experiments to evaluate the importance of forb abundance in brood habitat (see Chapter 3). The field exposure sites were known brood sites with 3 levels of forb abundance (i.e., < 10%, 10 -

20%, and > 20%). These sites were randomly selected from brood sites identified during the 2 years prior to the studies by monitoring the movements of radio-collared hens with broods.

The 2002 study began on Day 2 and continued for 27 days (May 27 - June 22). Each morning the chicks were transported to an exposure area and released between 0730 and 0830 (1-2 hours after sunrise). The chicks were transported in the brooders until they became too large; thereafter, they were transported in subdivided cardboard boxes with a cloth tops. The chicks were allowed to feed until they returned to the brooder in the evening between 1830 and 2130, depending on the weather and the age of the chicks. This schedule resulted in 10 to 14 hours of feeding opportunity per day. The chicks were given access to a brooder the entire time they were in the field and to water from Day 7 until the end of the study.

Feeding observations, lasting 10 minutes each, were conducted 3 times an hour during 8 hours of the day. During these periods, the observers closely followed an individual chick and recorded its activity (e.g., feeding, loafing, brooding, or dusting), and the duration of each activity using a palmtop computer. During active feeding, the peck rate and items pecked were recorded. The observers vocalized during these feeding observations and were followed by the other chicks. Weather conditions and temperature were recorded at each site, 4 to 6 times each day.

The field exposure methods in 2003 were the same as in 2002, with 4 exceptions. First, the duration of the study was extended from 27 days to 54 days (May 22 - July 14). Second, in order to increase the feeding opportunity to 14 - 16 hours per day, the chicks were released between 0530 and 0600 each morning and remained at the sites until 2000 to 2130 each evening. Third, the chicks were given access to water the entire time they were in the field. Last, the feeding observation protocol was changed due to concerns that the methods used in 2002 resulted in excessive daily movements and provided uninformative data. Feeding observations were only conducted on 18 of the 54 days (i.e., Days 4-6, 13-15, 22 - 24, 31 - 33, 40 - 42, and 49 - 51). Each chick was observed for 1, 5-minute period per day. During these observations, the observers remained at least 2.5 m away from the chicks and recorded only the substrate (i.e., soil,

grass, forb, sagebrush (*Artemesia tridentata*), rabbitbrush (*Chrysothamnus spp.*)) at which the chicks pecked. In order to expose the chicks to the entire exposure area each day, the observers changed locations periodically.

Mass and feather length were used as indicators of the quantity and quality of appropriate forage available at the sites in relation to the nutritional needs of the chicks. Each chick was weighed and physically examined each morning of the field exposures. The seventh primary feather of the right wing was measured every morning in 2002 and every third evening in 2003. In 2003, the masses and primary lengths of the study chicks were compared to those of wild sagegrouse chicks at hatch and on Day 50. Measurements of wild sage-grouse chicks in the study area during the study were acquired as part of a separate study on chick mortality. These chicks were captured and weighed within 1 day of hatching and radio transmitters were sutured to their backs. The surviving chicks were recaptured and measured at 40-60 days old.

Housing

The chicks were in the field during each day of the study and, therefore, only required housing at night. The chicks were housed in the brooders for approximately the first 2 weeks. During Weeks 2 to 5 the chicks were housed in the imprinting ring covered with a bedsheet to contain them. During this period, the brooders were placed inside the imprinting ring so that the chicks could behaviorally thermoregulate by entering and exiting them. Water dishes were also placed inside the ring. After Week 5, the chicks were housed in wood frame wire cages. Water was placed in the cages and the floors were lined with newspaper. Each of the housing units was cleaned thoroughly daily in order to reduce the risk of disease outbreaks. The chicks were not given any antibiotics or nutritional supplements during the study.

Initially the housing units were centrally located and all of the chicks were brought back to this location each day. In 2003, due to concerns over the stress caused by transportation, field housing units were set up at the most distant exposure sites. Field housing units consisted of the

housing units described above (i.e., brooders, imprinting rings and cages) placed inside enclosed field vehicles to exclude predators. These vehicles were parked at the exposure sites.

RESULTS

Egg Acquisition

Forty-four eggs were collected between 18 and 27 April 2002. Thirty-nine of these eggs were collected from 6 nests in Middle Park. Four of the 6 hens renested; each renest contained 6 eggs. One of the hens was depredated before a renest was found and the remaining hen did not renest. In addition to the eggs collected in Middle Park, 4 eggs were collected from an abandoned nest of an uncollared hen in Moffat County, CO. The renesting status of this hen is unknown because she was uncollared. In addition, a single egg was taken from a radio-collared hen in Moffat County. The rest of the nest was left undisturbed and the hen continued to incubate the remaining eggs.

Sixty-eight eggs were collected between 13 and 21 April 2003 from 8 nests in Moffat County, CO. All of the eggs were collected from within the study area in order to eliminate the possibility of introducing disease and genetic material into the study population. The renesting status of these hens was not checked until 3-4 weeks after the simulated depredation of the original nests. At that time, 5 of the 8 hens were found to have renested. This represents the minimum number of renests due to possibility that renests were depredated during the intervening 3-4 weeks.

All eggs were collected from adult hens. None of these hens abandoned their nests as a result of egg collection and each continued to lay according to the normal pattern until the simulated depredation event. This lack of abandonment was even observed in hens that were flushed from the nest several times during egg collection. In 2002, 1 hen was flushed once from her nest. In 2003, 2, 1 and 3 birds were flushed once, twice and thrice, respectively, from their nests.

Egg Storage

The mean storage duration in 2002 and 2003 was 3 days (range = 0 - 9 days) and 9 days (range = 3 - 11 days), respectively. In 2002, the nests were located earlier in laying than in 2003, so that the estimated mean age of the eggs when placed in the incubator was 7 days (range = 1 - 16 days) in 2002 and 13 days (range = 3 - 22 days) in 2003.

Incubation and Hatching

The mean incubation time in 2002 and 2003, was 27.1 days (range = 26.5 - 27.9 days) and 25.8 days (range = 24.2 - 27.3 days), respectively. In 2002, 36 of the 44 (0.82, SE = 0.06) eggs hatched. One egg was infertile. The single egg from Moffat County was more developed than the others for the first 6-9 days of incubation and then stopped developing and died. This pattern of development is consistent with an egg that had started to develop before being placed in the incubator, either by the hen prior to collection or because of improper storage after collection. In 2003, 46 of the 68 eggs (0.68, SE = 0.06) hatched. No eggs were infertile.

No evidence was found that egg volume, egg collection mass or egg density affected hatchability (Table 1.1). The model without an egg volume effect had more support than the model with an egg volume effect. The "egg volume effect" model had 1 more parameter than the "no effect" model and the ΔAIC_C was 2.1, indicating that the addition of the volume effect parameter did not improve the model. This was also the case for the models that included effects for egg mass and egg density.

Although the model with a storage duration effect was better than the model without a storage duration effect, the ΔAIC_C was only 0.2, and the Akaike weight of the former model was only 0.53. This indicates that the evidence supporting this effect was weak. In addition, the slope parameter for the model with a storage duration effect was - 0.10 (95% CI = -0.24 to 0.03). The fact that 95% confidence interval overlaps 0, again indicates a lack of evidence for a storage duration effect.

Imprinting

The success of imprinting was evaluated on the afternoon of Day 1 when the chicks were released at a brood site. During this initial field exposure (and during subsequent field exposures), brood integrity was maintained through frequent contact calls issued by both the observers and the chicks. The contact calls used by the observers included calm speech and imitations of sage-grouse hen contact calls. Both worked equally well. When a chick strayed beyond audial and visual contact with the observer and brood, it gave distress calls and returned to the vicinity of the observer once contact was restored. Each of the chicks displayed this behavior and was, therefore, considered adequately imprinted for inclusion in the study. The chicks did not imprint on a single person, but rather on humans in general. This meant that several observers could be involved in the study. The chicks remained imprinted and responsive to the observers throughout the study, even after they could thermoregulate and fly, at which time they were less dependent on the observer for warmth and protection.

Chick Transport

During transport, bath towels were placed in the brooders for stability and cushioning. In 2003, 2 chicks died during transport over rough roads. These chicks may have been caught under the towel and trampled by the other chicks. In response, the towels were removed from the brooders and dividers were installed to prevent trampling. The chicks appeared to be stressed if alone in a compartment, dividers were, therefore, placed to allow 3 chicks per compartment. After these changes were made, there were no additional chick mortalities during transport. Transport, however, remained stressful to the chicks, as evidenced by the frequency and intensity of the distress calls given. This stress was reduced as much as possible by using the field housing units described above to reduce time spent in transport.

Field Exposures

The chicks were very proficient at using the brooders throughout the study, entering and exiting when needed to regulate their body temperatures. The success of imprinting and the chicks' ability to use the brooders allowed them to move unrestrained through the exposure sites.

In addition to the contact calls and distress calls used to maintain brood integrity, communication between the observers and the chicks included alarm calls given by the chicks in response to potential predators and hide calls (i.e., a trill) given by the observers in the presence of danger. Alarm calls issued by the chicks were usually the first indication that a predator was approaching and would cause all of the chicks to become alert. Hide calls resulted in the chicks dispersing by running for several feet and then taking cover under a sagebrush or other suitable vegetation.

Although the presence of an observers and their ability to communicate with the chicks prevented most predators from taking study chicks, 1 chick was depredated by a western rattlesnake (*Crotalus viridis*), another was probably killed by a weasel (*Mustela sp.*), and 2 were taken by golden eagles (*Aquila chrysaetos*). Several other avian predators and scavengers (golden eagles, American kestrels (*Falco sparverius*), loggerhead shrikes (*Lanius ludovicianus*), Swainson's hawks (*Buteo swainsoni*), red-tailed hawks (*Buteo jamaicensis*), northern harriers (*Circus cyaneus*), turkey vultures (*Cathartes aura*), and various corvids) were commonly observed at or near the exposure sites, however, none of them were successful in taking a study chick. Several chicks less than 10-days-old became entangled in viscous leaves of rabbitbrush to such a degree that they had to be freed by the observers. In a concurrent study in the study area, 2 wild sage-grouse chicks with radio transmitters were found to have died after becoming entangled in rabbitbrush.

Wild broods were often observed in or near the study sites. The response of a wild hen to our presence varied from leading her own chicks out of the area, to aggressively approaching the observer and persistently trying to gather the human-imprinted chicks.

The chicks returned to the observer to roost each evening. During the first 6 weeks, if given enough time and encouragement, the chicks would enter the brooder upon return. After 7 weeks, several of the chicks returned to the vicinity of the observer to roost under a sagebrush instead of entering the brooder. After they began to roost, they discontinued all contact and distress calls and would not respond to the observer's calls, making them difficult to locate. On 3 occasions, this resulted in the chick being left at the site overnight. In each of these cases, the chick returned to the observer in the morning and rejoined the brood.

Feeding activity

Upon release in the field, the chicks dispersed and moved quickly and erratically through the habitat as they fed. The chicks did not appear to be disturbed by the observers' presence. It was, therefore, possible to record information on the chicks' daily time budgets, food selection, and behavior as they moved unrestrained through brood areas. However, due to the rapid pace at which the chicks moved and the small size of the items at which they pecked, it was usually not possible to distinguish successful from unsuccessful pecks especially when directed at invertebrates. The peck rate data recorded during 2002 was, therefore, considered uninformative and unreliable. In 2003, it was possible to successfully record the substrates at which the chicks pecked. The mean proportions of pecks in 2003 that were directed at each of the substrates during the early brood period, the late brood period and the 2 periods combined are shown in Table 1.2.

During the mornings and evenings, feeding was continuous. In the middle of the day, the chicks often suspended feeding and returned to the observer to loaf, preen, dust bathe, drink water, sleep or brood. The dispersal distance during active feeding depended on the age of the chicks, with younger chicks remaining closer to the observer than older chicks, and on the ability of the chick to maintain contact with the other chicks and the observer. In sparse vegetation with

the observer speaking loudly and standing erect, the chicks would disperse farther than in dense vegetation with the observer speaking softly and remaining close to the ground.

During the first week of the study the chicks fed predominantly on invertebrates. The amount of invertebrates ingested steadily decreased while the amount of forbs steadily increased so that by the end of the study in 2003 (Day 54) forbs dominated the diet of the chicks.

Throughout the study, the chicks fed predominantly on plants for the first 15 minutes after being released in the mornings and before entering the brooders to brood or roost. Table 1.3 lists the items positively identified as consumed by the chicks. Several of these forb species were preferentially ingest by the chicks when present. These included *Androsace septentrionalis* (northern rock jasmine), *Calochortus nuttallii* (sego lily), *Collinsia parviflora* (maiden blue-eyed Mary), *Mertensia oblongifolia* (bluebells), *Trifolium spp.* (clover), and several members of the Asteraceae family, including *Agoseris glauca* (false dandelion), *Crepis intermedia* (gray hawksbeard), *Erigeron filifolius* (threadleaf fleabane), *Taraxacum officinale* (common dandelion), *Townsendia hookeri* (Hooker's Townsend daisy), and *Tragopogon dubius* (salsify). Chicks ingested the leaves and entire closed flower heads, but rarely ate the opened flower heads of these Asters.

Forb species that were rarely ingested by the chicks, even though they were commonly present at the exposure sites included *Allium spp.* (wild onion) and *Castilleja spp.* (indian paintbrush). Similarly, the forb species that were never or extremely rarely ingested, even though they were commonly present, were *Alyssum alyssoides* (pale madwort), *Alyssum desertorum* (desert madwort), *Antenaria spp.* (pussytoes), *Delphinium bicolor* (low larkspur), *Erigonum umbellatum* (sulphur-flower buckwheat), *Lupinus spp.* (lupine), *Penstemon caespitosus.*(mat penstemon), *Phlox hoodii* (moss phlox), *Rannunculus testiculatus* (burr buttercup), *Senecio spp.* Chicks ingested grasses extremely rarely.

Most of the items in Table 1.3 were eaten when available at the exposure sites. However, although *Balsamorhiza sagittata* (arrowleaf balsamroot), *Artemesia tridentata* (big sagebrush)

and Achillea millefolium (yarrow) were present throughout the study, the chicks did not begin eating these plants until Days 21, 21, and 35 respectively. When feeding on sagebrush the chicks preferred young plants and new growth.

Invertebrate forage included cicadas, grasshoppers, ants, mosquitoes, beetles, spiders, moths, butterflies, grubs, aphids and caterpillars without abundant setae (e.g., inchworms). During cicada hatches, the chicks consumed up to 10 cicadas per hour, constituting a large portion of forage during those times. Chicks avoided certain beetles (e.g., stinkbugs), all caterpillars with abundant setae (*Malacosoma spp.*), and certain ants. The chicks ate invertebrates from the ground, forbs, shrubs, and grass. During 2002, a majority of the pecks during the first 2 weeks were directed at aphids and ants on sagebrush and rabbitbrush. This may have been due to a lack of other sources of invertebrate forage. In 2002, the sagebrush may have, therefore, provided invertebrate forage where other sources had failed. This was not observed in 2003, during which very few pecks were directed at sagebrush or rabbitbrush in the first 2 weeks.

With the exception of large invertebrates (e.g., grasshoppers), which took up to 30 minutes of continual pecking to break up and ingest, chicks younger than 3 weeks of age did not direct numerous consecutive pecks at any food source. In contrast, after 3 weeks of age, chicks often pecked at one food source for several consecutive minutes, until the source was completely consumed. This was particularly evident when pecking at ant colonies, clover and dandelions.

Mass and feather length

We were able to easily collect mass and feather length data throughout the study with little struggle or apparent stress to the chicks. The mean mass, mean feather length and corresponding 95% confidence intervals of 50-day-old human-imprinted chicks in the 3 treatment groups and of 50-day-old wild chicks in the study area (Colorado Division of Wildlife, unpublished data) are shown in Table 1.4.

Mortality

In 2002, 27 of the 36 chicks died during the 29 day study; a mortality rate of 0.75 (SE = 0.07). Three chicks died from congenital deformities (Day 1, 4, and 4). During field exposures, there was 1 confirmed case of depredation (Day 5). Nine additional chicks disappeared during field exposure (Day 5, 5, 5, 5, 6, 9, 11, and 17). Given the strength of imprinting and observed behavior, all of these chicks were assumed to have died of depredation or malnutrition, rather than having strayed and become lost. Malnutrition was the suspected cause of death for the remaining 14 chicks (Day 4, 4, 5, 6, 6, 6, 6, 6, 7, 8, 9, 10, 10, and 11).

In 2003, the mortality rate during the 54-day study, excluding chicks that died due to human-error, was 0.32 (SE = 0.07, n = 41). Two chicks were killed by golden eagles (Day 8 and 18), 1 was depredated by a rattlesnake (Day 13), 5 chick disappeared in the field (Day 4, 9, 17, 20, and 26), 1 died from a ruptured yolk sac (Day 3), 5 died after appearing weak and lethargic for a day (Day 4, 10, 15, 22, and 26), 2 were stepped on by the observers (Day 1 and 6) and 2 died from injuries sustained during transport (Day 12 and 14).

CONCLUSIONS

Evaluation of Methods

The use of human-imprinted chicks has been shown in previous studies to be a valuable tool in brood habitat studies with several gallinaceous species. This study has shown, for the first time, that this approach is also suitable for use with sage-grouse. The attainment of the desired number of chicks indicated that the egg collection, storage and incubation methods used were effective. The ability of the observers to closely monitor the growth, development, and feeding activities of the chicks in brood habitat showed that the imprinting and field exposure methods used were successful. The appropriateness of the site selection method was confirmed by the fact that wild broods were often observed in several of the study sites during field exposures. The

lack of cannibalism and disease showed that the animal care, housing, and field exposure methods were suitable.

Mass and feather length were informative response variables in assessing the effects of forb abundance on sage-grouse chicks. Feeding activity measurements (e.g., peck rate, food item selection, feeding duration) were considered unreliable and uninformative because the quick pace of feeding and the visual obstruction caused by the vegetation made it difficult to distinguish successful from unsuccessful pecks. Similar conclusions were made by Palmer (2001) working with bobwhite quail and by Hunter (1985) working with ducks.

The longer incubation time in 2002 may have been due to a thermometer malfunction that led to the incubator temperature being 0.8 °C too low for the first 2.5 days (Harvey 1993). The wider range in incubation duration in 2003 may have been due to the greater number of eggs and the increased age of the eggs (Cartwright, 2000). The lower hatch rate in 2003 may have been due to the greater age of the eggs when placed in the incubator (Cartwright 2000, Harvey 1993). I was unable to evaluate the effect of egg age on incubation duration and hatchability because the ages of the individual eggs when placed in the incubator were not known. Egg age was a function of the number of days the egg spent in the nest before collection and the number of days stored after collection. The storage duration was known precisely for each egg and there was some evidence that hatchability decreased as storage duration increased. The age at collection for most eggs, however, was not known because many of the nests contained several eggs when found. It was impossible to determine the order in which these eggs had been laid and, therefore, the ages of the individual eggs at collection.

Wild chicks in the study area in 2003 were heavier at 50-days-old than the human-imprinted chicks. In addition, the wild chicks had longer primary feathers than the human-imprinted chicks exposed to brood areas with < 20% forb abundance, but not longer than those of chicks exposed to brood areas with > 20% forb abundance. The lower growth rates of the human-imprinted chicks may have been due to their restricted daily feeding opportunity, the

increased energetic stress during transport, or differences in the way the human-imprinted and wild chicks were exposed to the habitat. Although the absolute effect of forb abundance on the growth of wild chicks and the human-imprinted chicks may, therefore, not be equal, the relative effects of forb abundance on the growth of the human-imprinted chicks is probably indicative of that of wild chicks. In future studies, it may be informative to compare the body composition of human-imprinted chicks to wild chicks as an indicator of dramatic differences between the nutritional intakes of the 2 groups.

Crawford and Gregg (2001) reported a mortality rate in wild chicks at 28 days in Oregon of 0.61 (SE = 0.04 calculated from source). This mortality rate was not statistically different than that observed in the human-imprinted chicks in 2002 (0.75, SE = 0.07). This wild chick mortality rate was, however, 1.9 times higher than that observed in 2003 (0.32, SE=0.07). The human-imprinted chick mortality rate in 2002 was 2.3 times higher than in 2003. The majority of mortality in 2002 was a result of malnutrition. This malnutrition may have been due to inadequate invertebrate forage in 2002, during which a large proportion of pecks during the first 2 weeks were directed at aphids. This dependence on aphids was not observed in 2003. Borg (2000) reported that aphids were not adequate to sustain gray partridge growth. This suggests that the chicks in 2002 may have relied on aphids because there was inadequate alternative invertebrate forage.

Study design may also have contributed to chick malnutrition in 2002. Two changes were made to the field exposure methods after the 2002 study in an attempt to decrease malnutrition. These were an increase in the daily exposure time from 12 to 16 hours and a discontinuation of the feeding observations, which decreased the distance traveled by the chicks per day. In addition, in 2003 the chicks were first exposed to sagebrush habitat on Day 0 instead of Day 1. This may have allowed them to more appropriately select food items 1 day earlier than the chicks in 2002. There were other differences in the 2002 and 2003 studies including location, climate, and chick source population. Although it is not possible to know which of these

differences led to the decreased mortality in 2003, this result may suggest that 12 hours of continuous feeding opportunity per day is not sufficient if chicks are not offered supplementary food. It may also suggest that feeding observations that result in extensive travel distances are not appropriate for studies on sage-grouse.

Human-Imprinted Chicks as Surrogates for Wild Chicks

Inference from the human-imprinted chicks in this study to wild chicks required the assumption that the study chicks responded, in terms of growth, to forb abundance in brood areas in a similar way as wild chicks. If the imprinting process or the exposure methods had led to substantial differences in the way human-imprinted chicks and wild chicks interact with their environment, this assumption would not have been met. These differences were thought to be small given that previous studies have indicated that imprinting precocial chicks to humans does not alter the chicks' basic behavior (Healy et al. 1975). Previous authors have concluded that gallinaceous chicks of several species are not fed nor taught to feed by the hen (Zwickel 1967, Healy et al. 1975, Kimmel and Healy 1987, Savory 1989, Palmer et al. 2001) and that imprinted chicks of these species instinctively select similar foods and exhibit similar foraging behavior as wild chicks (Healy 1978, Kimmel and Healy 1987, Sharpe et al. 1998, Palmer et al. 2001). The food items selected by the human-imprinted chicks in this study and the timing of selection were very similar to that reported in studies which examined the crop contents of wild sage-grouse chicks (Klebenow and Gray 1968, Klebenow 1969, Peterson 1970, Drut et al. 1994b). One exception was that none of these studies reported that wild sage-grouse chicks ingested aphids. In 2002, the majority of pecks for the first 2 weeks were directed at aphids. This discrepancy may have been due to the inability to identify aphids in crop contents. In a study with humanimprinted chicks, Kimmel and Samuels (1978) observed ruffed grouse ingesting aphids.

The chicks in this study fed actively in the mornings and the evenings and loafed during midday; similar behavior was reported in wild chicks (Gill 1965, Autenrieth 1981, Sveum et al.

1998). The similarities in food selection and daily time budgets suggested that human-imprinted sage-grouse chicks feed similarly to wild chicks. Healy (1978) found that human-imprinted turkey poults followed the experimenter in a manner similar to that of wild poults following a hen. The dispersal, movement, communication, brooding behavior and flight ability exhibited by the human-imprinted chicks in this study were similar to those anecdotally described in wild sage-grouse (Patterson 1952), blue grouse (Zwickel 1967) and willow ptarmigan (Watson, 1972).

In conclusion, although the growth rates of the human-imprinted chicks were lower than those of wild chicks, the food selection, feeding behavior, communication, daily time budgets, and brooding behavior of the human-imprinted chicks in this study were similar to those of wild chicks reported in previous studies. The assumption that the human-imprinted chicks responded, in terms of growth, to forb abundance in brood areas in a similar way as wild chicks was, therefore, considered acceptable.

Additional Applications and Future Research

The field exposure methods used in this study could be used to study several aspects of sage-grouse ecology on a variety of scales. These methods could be used to gain detailed information on chick biology, such as growth and development patterns, food selection, daily time budgets, predator avoidance, movement patterns, etc. Experiments could also be designed to study population specific concerns, such as the effects of distance traveled by broods in populations where extreme distances have been observed.

Previous studies have indicated relationships between specific habitat characteristics and sage-grouse presence and productivity. Human-imprinted chicks could be used in experiments to establish and quantify these relationships and to study the possible mechanisms behind them. In the current study, human-imprinted chicks were used to study the direct effects of forb abundance on the growth and development of chicks. This same method could be used to evaluate the importance of other resources to sage-grouse chicks or to study other chick response variables

(e.g., age at first flight, survival). Conventional brood habitat evaluation methods could be assessed and improved based on the information gained through these studies. For example, Palmer (2001) compared the rankings of bobwhite habitats based on several habitat evaluation methods including mass gain of human-imprinted chicks.

Management agencies often treat expanses of sagebrush with the primary or subsequent goal of improving these areas for the benefit of sage-grouse. Human-imprinted chicks could be used to evaluate and improve the effectiveness of individual treatment methods or to rank several available treatment methods. In addition, the quality of known brood areas could be evaluated as could the suitability of potential brood areas prior to the reintroduction of sage-grouse. This information could be used in cost-benefit analyses and in prioritizing management actions.

Sharpe et al. (1998) released human-imprinted ruffed grouse and was able to approach and observe them feeding for up to 1.5 years. Similarly, Kimmel (1987) reports that human-imprinted turkeys, released into the wild, exhibited normal nesting and brood rearing behavior and allowed human observation at less than 2 m without being disturbed. It may, therefore, be possible to study human-imprinted sage-grouse throughout their life cycle and in multigenerational studies.

The chick acquisition and imprinting methods described in this paper could also be used to provide subjects for laboratory studies. These methods provide equal-aged chicks, which are required by some experimental designs. In addition, human-imprinted chicks are easier to maintain and handle and they experience less stress in captivity than wild birds. This results in fewer incidences of disease and injury (Kimmel 1987).

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Table 1.1: Model selection results for the effect of egg volume, egg collection mass, egg density and storage duration on the hatchability of artificially incubated sage-grouse eggs from Middle Park and Moffat County, Colorado in 2002 and 2003, respectively.

Model	n	K	log (L)	AIC _c	Δ	w_i
Volume						
No effect	111	2	-63.8	131.6	0	0.74
Volume	111	3	-63.8	133.7	2.1	0.26
Density						
No effect	111	2	-63.8	131.6	0	0.74
Density	111	3	-63.8	133.7	2.1	0.26
Collection Mass						
No effect	111	2	-63.8	131.6	0	0.74
Collection Mass	111	3	-63.7	133.7	2.1	0.26
Storage Duration						
No Effect	111	2	-63.8	131.6	0.2	0.47
Storage Duration	111	3	-62.6	131.4	0.0	0.53

Table 1.2: Mean proportion of pecks directed at each substrate (i.e., soil, forbs, grass, sagebrush and rabbitbrush) during the early brood period (May 22 - June 17), late brood period (June 17 – July 14) and overall by human-imprinted sage-grouse chicks in Moffat County, Colorado in 2003.

The Control of	Early brood period		Late brood period		Overall	
Substrate	Mean (%)	(95% CI)	Mean (%)	(95% CI)	Mean (%)	(95% CI)
Soil	45	(40 - 49)	51	(37 - 64)	48	(41 - 54)
Forb	32	(29 - 35)	34	(21 - 48)	33	(27 - 39)
Grass	10	(6 - 14)	13	(11 - 16)	12	(10 - 14)
Sagebrush	9	(6 - 12)	1	(0 - 1)	5	(2 - 7)
Rabbitbrush	4	(2 - 5)	0	(0 - 0)	2	(1 - 3)

Table 1.3: Forbs and invertebrates eaten by human-imprinted sage-grouse chicks exposed to brood areas of Middle Park and Moffat County, CO in 2002 and 2003, respectively.

Scientific name	Common name	Plant part eaten	
<u>Forb</u>			
Achillea millefolium	Yarrow	Leaves	
Agoseris glauca	False dandelion	Leaves, closed flowers	
Allium spp.	Wild onion	Flowers	
Androsace septentrionalis	Northern rock jasmine	Flowers, seeds	
Aster campestris	Western meadow aster	Flowers	
Astragalus spp.	Milkvetch	Flowers, developing seed	
Astragalus miser	Weedy milkvetch	Flowers, developing seed	
Astragolus convallarius	Lesser rushy milkvetch	Flowers developing seed	
Balsamorhiza sagittata	Arrowleaf balsamroot	Leaves	
Brassica spp.	Annual mustards	Flowers	
Calochortus nuttallii	Sego lily	Flowers, stems	
Castilleja spp.	Indian paintbrush	Leaves	
Collinsia parviflora	Maiden blue-eyed Mary	Flowers, seed	
Collomia linearis	Narrow leafed collomia	Leaves, flowers	
Crepis intermedium	Gray hawksbeard	Leaves, closed flowers	
Descurainia sophia	Tansy mustard	Siliques, leaves, flowers	
Erigeron engelmannii	Engelmann's fleabane	Leaves, closed flowers	
Erigeron filifolius	Threadleaf daisy	Leaves, closed flowers	
Lactuca serriola	Prickly lettuce	Leaves	

Scientific name	Common name	Plant part eaten	
Linum lewisii	Western blue flax	Flowers	
Lomatium orientale	Salt-and-pepper parsley	Developing seeds	
Medicago sativa	Alfalfa	Leaves	
Melilotus officinalis	Yellow sweet clover	Leaves	
Mertensia oblongifolia	Bluebell	Flowers, leaves	
Phlox longifolia	Phlox	Flowers	
Taraxacum officinale	Dandelion	Leaves, closed flowers	
Townsendia hookeri	Hooker's Townsend daisy	Leaves, closed flowers	
Tragapogan dubius	Salsify	Buds, leaves	
Trifolium fragiferum	Strawberry clover	Leaves	
Vicia americana.	American vetch	Flowers, developing seed	
Viola nuttallii	Violet	Leaves	
<u>Invertebrates</u>			
Araneae	Spiders	Entire	
Coleoptera	Beetles	Entire	
Diptera	Mosquitoes, Flies	Entire	
Homoptera	Aphids, Cicadas	Entire	
Hymenoptera	Ants	Entire	
Lauidantana	Butterflies, Moths,		
Lepidoptera	Inchworms	Entire	
Orthoptera	Grasshoppers, Crickets	Entire	

Table 1.4: Mean mass and feather length of wild chicks and chicks in the high, medium and low treatment groups at 50 days.

			Mass	Feather length		
Group	n	g	(95% CI)	mm	(95% CI)	
Wild	11	679	(603 - 755)	162	(157 - 166)	
High	6	498	(442 - 553)	156	(152 - 160)	
Medium	10	378	(334 - 423)	150	(144 - 155)	
Low	12	299	(277 - 321)	137	(133 - 141)	



Fig. 1.1: Portable brooder used during field exposures of human-imprinted sage-grouse chicks to brood areas of Middle Park and Moffat Count, Colorado in 2002 and 2003, respectively. Note the entrance at the lower right and the backpack, on top, for transport.

EVALUATING THE IMPORTANCE OF FORBS TO SAGE-GROUSE USING HUMAN-IMPRINTED CHICKS

ABSTRACT

Greater sage-grouse (Centrocercus urophasianus) populations are experiencing long-term declines throughout their current range. Several authors have suggested that the quality and availability of brood habitat may be limiting populations through reductions in the recruitment of young. In order to effectively manage brood areas, reliable information is needed on chick resource requirements and the role of various components of the habitat in chick growth, development and survival. Although several studies have indicated the importance of forbs in brood habitats, no studies have quantified the direct effects of forb abundance on sage-grouse chicks. In 2002 and 2003, I conducted field experiments in Middle Park and Moffat County, Colorado, respectively. The objective of these studies was to quantify the effects of 3 levels of forb abundance (i.e., < 10%, 10 - 20%, and > 20%) in brood habitat on the mass gain and feather growth of human-imprinted sage-grouse chicks. In 2002, there was no evidence that forb abundance in the exposure areas had an effect on either of these response variables. However, in 2003, the mass gain and feather growth rate of chicks increased with forb abundance. Previous studies have shown a correlation between chick mass and long-term survival. Management actions that increase forb abundance in brood areas with < 20% forb abundance may, therefore, lead to increased chick survival and grouse productivity.

INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*) populations are experiencing longterm declines throughout the current range of the species (Connelly and Braun 1997). Concern over these population declines has led to conservation efforts at regional, state, and local levels. Several authors have suggested that the quality and availability of brood habitat may be limiting populations through reductions in the recruitment of young (Drut et al. 1994 *a* and *b*, Connelly and Braun 1997, Sveum et al. 1998). In order to effectively manage brood areas, reliable information is needed on chick resource requirements and the role these resources play in chick growth, development and survival. Previous studies have indicated that forbs are an important resource for chicks by showing correlations between forb abundance in brood habitat and brood success (Autenrieth 1981), and productivity (Drut et al. 1994*b*). Similarly, studies have suggested that forbs play a role in brood habitat selection (Klebenow 1969, Wallestad 1971, Drut et al. 1994*a*, Sveum et al. 1998), brood movements (Klebenow 1969, Wallestad 1971, Autenrieth 1981), distribution (Peterson 1970, Wallestad 1971), and home range size (Drut et al. 1994*a*).

The most commonly proposed mechanism behind these relationships is the influence that forbs have on the forage quality of brood habitat. Forbs and invertebrates dominate the diet of wild sage-grouse chicks for the first 12 weeks of life (Klebenow and Gary 1968, Peterson 1970). Forbs are important forage for sage-grouse chicks because they contain higher proportions of energy, calcium and vitamin C than invertebrate forage (Bernard and Allen 1997, Barnet 1994, Savory 1989). Invertebrates contain higher concentrations of protein, sulfur-amino acids, phosphorus and most vitamins (especially B₁₂) than forbs (Bernard and Allen 1997, Barnet 1994, Savory 1989). Invertebrate forage provides concentrations of proteins and sulfur-amino acids necessary for chicks to develop the muscles and feathers required for flight, whereas plant forage does not (Savory 1989). In laboratory studies, Johnson and Boyce (1990) showed that chick growth and survival rates increased with the quantity of invertebrates in the diet and that invertebrate forage was required for survival until chicks are at least 21-days old. Similarly, Jorgensen and Blix (1985) found that both growth and survival rates of captive willow ptarmigan (*Lagopus lagopus*) chicks increased with the protein concentration of their food.

Although both forbs and invertebrates are known to be important forage for sage-grouse chicks, the current study focused only on forb abundance. Invertebrate abundance was not studied for several reasons. Firstly, management agencies commonly manage the vegetative component of sage-grouse habitat, whereas management of the invertebrate component is less common. Secondly, invertebrate abundance is thought to generally increase with increasing forb abundance (Blenden 1986, Brush 1986). Thirdly, standard entomological sampling techniques do not account for invertebrate availability to chicks and, therefore, produce data that is not biologically relevant (Palmer 2001).

Previous studies have indicated that forbs in brood habitats influence chick movements, growth, and survival; however, no studies have directly quantified the effects of forb abundance in brood areas on sage-grouse chicks. In 2002 and 2003, I conducted field experiments in Middle Park and Moffat County, Colorado, respectively. The objective of these experiments was to quantify the effects of forb abundance in brood habitat on the growth of sage-grouse chicks. In pursuit of this objective, human-imprinted sage-grouse chicks were exposed to known brood sites with 3 levels of forb abundance (i.e., < 10%, 10 - 20%, and >20%) and their mass and feather growth were monitored. In this paper, I describe these experiments, their results and management implications.

STUDY AREAS

Middle Park, CO

Middle Park is an intermountain basin located primarily in Grand and Summit counties of Colorado. This basin is bounded to the North by the Rabbit Ears and Never Summer Ranges, to the East by the continental divide, to the South by the Williams Fork and Vasquez Ranges, and to the West by the Gore and Park Ranges (Tiedeman et al. 1987). The principal drainage is the Colorado River, which runs from east to west through the middle of the park. The Blue and

Williams Fork rivers are tributaries that drain the southern portion of the park; the Willow, Troublesome and Muddy creeks drain the northern portions (Potter and Braun 1999).

This study was restricted to the section of Middle Park west of Byers canyon. This area of the park lies within the rain shadow of the mountains that surround it. The climate is characterized by long, cold winters and brief, cool summers with afternoon thundershowers. The 40-year mean annual precipitation and temperature recorded in Kremmling were 29.2 cm and 3.6 C°, respectively. The annual precipitation and temperature in 2002 were 27.2 cm and 3.5 C°, respectively (Western Regional Climate Center, 2003). At elevations of 2200 to 2750m, the vegetation was dominated by Wyoming and mountain big sagebrush (*Artemisia tridentata wyomingensis* and *A. t. vaseyana*, respectively) (Tiedeman et al. 1987).

Axial Basin and Danforth Hills of Moffat County, CO

The Axial Basin and Danforth Hills are located in Moffat County, 30 km southwest of Craig, CO. The principle drainage is the Yampa River, which flows from east to west through the Axial basin. The Axial Basin consists primarily of private, state and federal rangeland at elevations of 1,800 to 2,000m. The Danforth Hills are a series of North-South ridges located adjacent to and south of the Axial Basin. The northernmost area of the Danforth Hills was used in this study. This area is owned by the coal mining industry and ranges in elevations from 2,000 to 2,350 m. The 25-year mean annual precipitation and temperature recorded at the Craig 4SW climate station was 40.6 cm and 6.1 C° (Western Regional Climate Center, 2003).

The shrub community was dominated by big sagebrush (*A. t. wyomingensis* in the Axial Basin and *A. t. vaseyana* at higher elevations). The predominant grasses included western wheatgrass (*Pascopyron smithii*), Kentucky bluegrass (*Poa pratensis*), Sandberg bluegrass (*Poa secunda*), cheatgrass brome (*Bromus tectorum*), and needle and thread grass (*Hespero-stipa comata*). Dominant forbs included lupine (*Lupinus sericeus*), wild onion (*Allium sp.*), arrowleaf balsamroot (*Balsamorhiza sagittata*), and varrow (*Achillea millefolium*) (Hausleitner 2003).

METHODS

Selection of Exposure Sites

and 2001 by monitoring the movements of radio-collared hens with broods. Each of these brood sites was located in upland sagebrush. Each site was visited in the spring of 2002 in order to categorize them according to forb abundance. Sites that were estimated to have less than 10% forb cover were placed in the low-forb-abundance category; sites with 10-20% forb cover were placed in the medium-forb-abundance category; and those more than 20% forb cover in the high-forb-abundance category. This resulted in 5 sites in each forb abundance category. Three of the 5 sites in each category were randomly selected for use in this study. An area of approximately 700 m² surrounding each of the selected brood sites, with vegetation similar to that of the exact brood site, was demarcated with flagging and served as an exposure area. Drut et al. (1994a) suggested that 12-14% forb cover may be the minimum forb abundance required for sage-grouse brood habitat. Likewise, the greater sage-grouse habitat guidelines (Connelly et al. 2000) recommend that early-brood habitat have at least 15% forb cover. The forb abundance categories used in this study, therefore, were chosen to provide information on how chicks responded to sites with forb abundance levels below, equal to, and above the recommended levels.

The exposure sites in 2003 were randomly selected from over 300 brood sites in Moffat County, CO that had been identified during the spring and summer of 2001 and 2002 by monitoring the movements of radio-collared hens with broods. These locations were divided into early and late-brood use sites, the former were used by chicks less than 1 month old and the latter by chicks greater than 1 month old. The early-brood areas were randomly ordered. These locations were visited in the order dictated by random assignment and categorized according to forb abundance until the required number of suitable locations in each category had been identified. The same categorization was used in 2003 as in 2002. All early-brood sites not

dominated by sagebrush were discarded. The late-brood sites were selected in the same way as the early brood sites, with one exception; sites not dominated by sagebrush were not discarded. Late-brood sites, therefore, included sagebrush dominated areas, areas where the sagebrush had been burnt off, meadows and conservation reserve program areas.

Acquisition of Human-imprinted Chicks

Protocols for the use of sage-grouse chicks in this study were approved by the Colorado State University (02-023A-01) and the Colorado Division of Wildlife Animal Care and Use Committees. Chicks were acquired and imprinted to humans by the methods described in Chapter 2. Briefly, sage-grouse eggs were collected from the nests of wild hens. These eggs were stored until the required number had been collected and then incubated. The resulting chicks were imprinted to humans during the first 48 hours after hatching. During this period the chicks were also taught to use portable brooders and familiarized with upland sagebrush habitat. They were then randomly assigned to high, medium, and low-forb-abundance (hereafter high, medium and low) treatment groups with nest mates being balanced across treatment groups as much as possible.

Field Exposures

The 2002 study began on Day 2 (Day 0 being the mean hatch date) and continued for 27 days (May 27 - June 22). Each morning, the chicks in the low treatment group were transported to the predetermined low exposure site. Likewise the medium and high treatment groups were transported to medium and high exposure sites, respectively. The chicks were transported in the brooders until they became too large; thereafter, they were transported in subdivided cardboard boxes with cloth tops. The chicks were released between 0730 and 0830 (1-2 hours after sunrise) and allowed to feed until they returned to the brooder in the evening between 1830 and 2130, depending on the weather conditions and the age of the chicks. This schedule resulted in 10-14 hours of feeding opportunity per day. The chicks were given access to a brooder the entire time

they were in the field and to water from Day 7 on. Feeding observations, lasting 10 minutes each, were conducted 3 times an hour during 8 hours of the day. During these periods, the observers closely followed an individual chick while vocalizing continually to allow the other chicks to follow. Weather conditions and temperature were recorded at each site, 4 - 6 times each day. There were 3 exposure sites in each forb-abundance category. Each treatment group was exposed to the 3 appropriate exposure areas following a rotation schedule of 3 days on followed by 6 days off repeated 3 times.

The field exposure methods in 2003 were the same as in 2002, with 5 exceptions. First, the duration of the study was extended from 27 to 54 days (May 22 - July 14). Second, in order to increase the feeding opportunity to mean of 15 hours per day, the chicks were released between 0530 and 0600 each morning and remained at the sites until 2000 to 2130. Third, the feeding observations were discontinued due to concerns that they resulted in excessive daily movements. Instead, the observers changed locations periodically in a way that exposed the chicks to the entire exposure site each day. Fourth, the chicks were given access to water from Day 0. Finally, as in 2002, chicks were exposed to each site for 3 consecutive days, however, due to forb desiccation within the exposure sites, it was necessary to replace exposure sites in which the forb abundance had fallen below the minimum for the category. The chicks were therefore exposed to 5, 5, and 4 different low, medium, and high exposure sites, respectively, during the early-brood period and 4, 6, and 4 during the late-brood period.

The mass gain and physical condition of each chick was monitored closely. Interventions were made when the well-being of the chicks appeared to be in jeopardy. In 2002, the slow growth rates of the chicks raised malnutrition concerns on Day 6. In response, each chick was fed 1.8g of mealworms each morning on Days 7 - 14. This was reduced to 1g on Days 15-18 after which feeding was discontinued. In a study on captive 7 - 37 day old sage-grouse, Johnson and Boyce (1990) observed malnutrition in chicks fed 7.5g of invertebrates per day, but did not observe malnutrition in chicks fed 11.25g per day. The 1 and 1.8g of mealworms fed to the

chicks in this study were, therefore, estimated to be approximately 10 and 20% of the sustenance level. This level of supplementary feeding was thought to be adequate to prevent malnutrition, while still allowing the detection of a treatment effect.

Growth rates were considered adequate in 2003 for all but 1 chick, which was removed from the study on Day 24 after exhibiting a slow growth rate and appearing slightly lethargic. Each chick was fed 1g of mealworms on Day 10, when their release in the field was delayed by 7 hours.

Data Collection and Analysis

Forb Abundance of Exposure Sites.--In 2002, chicks were exposed to each of the 9 study sites 3 times for 3 days each. Vegetation sampling was carried out twice at each of these sites, once between the first and second visits and again following the third visit. Sampling was completed within 5 days of chick exposure. Although it would have been preferable to conduct vegetation sampling and chick exposures concurrently, this was not done due to the distraction it would have caused to the observers and the resulting increased probability of injuring or loosing a chick. In 2003, vegetation sampling was carried out at each of the early-brood sites within 5 days of chick exposure. The late-brood sites were sampled during chick exposures. By this age the chicks were large and active enough to effectively avoid being injured or lost during vegetation sampling.

In order to characterize the vegetation, 5 to 10 points, depending on the estimated variability, were randomly selected within each exposure site. The elevation, aspect, and slope of each point were recorded. A 20-m transect was then stretched in a randomly determined direction from each point. The composition of the overstory along each transect was recorded using the line-intercept method (Lucus and Seber 1977). The composition of the understory was determined by placing a 20-by-50-cm Daubenmire frame at 0, 5, 7.5, 10, 12.5, 17.5 and 20-m marks of the transect (Daubenmire 1959). The species of grass and forb present within each

microplot were then recorded along with an estimation of the percentage cover for total forbs, total grass and each forb species as well as for bare ground, soil, and litter.

The forb abundance along each transect was calculated by averaging the values of the 7 microplots. The mean forb abundance of each exposure site was then calculated by averaging the values from the individual transects. The overall forb abundance of each treatment category was calculated by averaging the forb abundances of the exposure sites within the category. The variances of at each step were calculated using the delta method.

Invertebrate Abundance of Exposure Sites.--In 2003, Geelhood (2003) studied the relationship between forb and arthropod abundance at the exposure sites. Invertebrate samples were collected by randomly placing 16 pitfall traps at each of the exposure sites. The contents of the traps were collected after 3 days, sorted to order and counted. Relationships were sought between forb abundance and (1) mean total number of invertebrates, (2) invertebrate order richness, and (3) abundance of each invertebrate order collected.

Mass Gain Rate.--Each chick was weighed within 0.1g each morning of the studies. As a result of the precision of the mass data, most of the variation observed in the data was considered to be the result of stochasticity in the growth process rather than of sampling or measurement error. In such situations, process error models more accurately estimate variances than sampling error models (White and Brisbin 1980). Process error models were, therefore, used to model the mass gain of the study chicks as a function of time, gender, and treatment. In both 2002 and 2003, the experiments ended before the chicks reached their asymptotic masses. The logistic functions commonly used to model growth (e.g., logistic, Richards', Gopertz and von Bertalanffy) could not, therefore, reliably be used to model the data. The following cubic polynomial function was used instead.

$$\beta_{0} + \beta_{1}t + \beta_{2}t^{2} + \beta_{3}t^{3} + \beta_{4}Gt + \beta_{5}Gt^{2} + \beta_{6}Gt^{3} + \beta_{7}Ht + \beta_{8}Ht^{2} + \beta_{9}Ht^{3} + \beta_{10}Lt + \beta_{11}Lt^{2} + \beta_{12}Lt^{3}$$

in which: t = Time

G = Gender

H = High forb-abundance treatment

L = Low forb-abundance treatment

In order to incorporate the error term appropriately, an additive discrete derivative process error model was developed in which the derivative of the above function was approximated by the following difference equation.

$$\frac{M_{i+1}-M_i}{t_{i+1}-t_i} = \beta_1 + 2\beta_2 t + 3\beta_3 t^2 + \beta_4 G + 2\beta_5 G t + 3\beta_6 G t^2 + \beta_7 H + 2\beta_8 H t + 3\beta_9 H t^2 + \beta_{10} L + 2\beta_{11} L t + 3\beta_{11} L t^2 + e_i$$

in which: M = Chick mass

i = Sampling time point

t = Time

G = Gender

H = High forb-abundance treatment

L = Low forb-abundance treatment

e = Error

The data from the 2 years were analyzed separately. Evidence for an effect of forb abundance on chick mass was sought using an information-theoretic approach (Burnham and Anderson 2002) in which 4 models were formulated (Table 2.1). Model $R_{\rm FG}$ represented the hypothesis that both forb abundance and gender affected the mass gain rate of chicks. Model $R_{\rm F}$ represented the hypothesis that forb abundance affected mass gain but gender did not. Model $R_{\rm G}$

represented the hypothesis that gender affected mass gain but forb abundance did not. Model R_o represented the hypothesis that neither forb abundance nor gender had an affect on the mass gain of chicks. Only chicks that survived until the end of the study were included in this analysis. The gender of each chick was determined through DNA analysis in 2003. Chick gender was not determined in 2002. Models $R_{\rm FG}$ and $R_{\rm G}$ were, therefore, not considered in 2002.

In 2003, the error variances increased with time. Equal error variances were achieved through a logarithmic transformation of the response variable (i.e., mass). In 2002, this transformation was not necessary.

The $AIC_{\mathbb{C}}$ value for each of these models was calculated using Proc Mixed in SAS (SAS Institute, Inc. 1999) with an autoregressive first order structure on the covariance matrices. In these models, time, forb abundance category, and gender were treated as fixed effects while chick was treated as a random effect. Comparison of the models was based on $AIC_{\mathbb{C}}$ values and Akaike weights. Model R_F was expected to be best supported by the data in 2002, while R_{FG} was expected to be best supported in 2003.

Evidence was sought for differences in the mass gain rates in 2002 and 2003 by compiling the data from 2002 and the first month of 2003 and comparing the AIC_C values of models R_o and R_Y (Table 2.1). Both models were additive process error models (White and Brisbin 1980) in which chick masses were modeled as a cubic polynomial function of time. Logarithmic transformation of the response variable was once again needed to achieve equal error variances. R_o represented the hypothesis that there was no appreciable difference in the mass gain rates between the 2002 and 2003. R_Y represented the hypothesis that there was a year effect on mass gain rates. Model R_Y was expected to be the best approximating model.

Feather Growth Rate.--The length of the seventh primary feather of the right wing was measured each morning in 2002 and every fourth evening in 2003. These feather growth data were analyzed in the same manner as the mass gain data described above. In 2002, the

autoregressive covariance structure was used. The increased time between feather measurements in 2003 led to a reduction in their autocorrelation. As a result the compound symmetric covariance structure was found to be better than the autoregressive structure. No transformation of the feather data was required.

Evidence for a year and treatment effect on feather growth rates was sought in the same manner as described above for the mass data. Of the treatment models, R_F was, again, expected to be best supported by the data in 2002, while R_{FG} was expected to be best supported in 2003. R_Y was expected to be the better of the year models.

Survival.--Although survival was not a primary response variable of interest in this study, mortality did occur. To evaluate the effects of forb abundance on chick survival, I modeled survival using known fate models in Program MARK (White and Burnham 1999). In this analysis, I formulated 4 models (Table 2.2). Model S_{fa} represented the hypothesis that forb abundance affected chick survival. Model S_{o} represented the hypothesis that forb abundance did not affect chick survival. Models S_{fa+m} and S_{m} incorporated daily chick mass as an individual covariate. Model S_{fa+m} represented the hypothesis that forb abundance affected survival. In model S_{m} , forb abundance did not affect chick survival. The best of these 4 models was identified based on AIC_{C} model selection (Burnham and Anderson 2002). This best model was used to estimate the probability of the chicks surviving until the end of the study. Gender was not used as a covariate in these models because the genders of the chicks that died before the end of the study were not known. All chicks that died from causes unrelated to the forb abundance of the exposure area (i.e., predation or mishandling) were censored from the analysis on the day of their death. Model S_{m} was expected to be best supported by the data.

I also used known fate models in Program MARK to compare chick survival in 2002 to that in 2003. In this analysis, 4 models were formulated (Table 2.2). Model S_Y represented the hypothesis that chick survival differed between the years. Model S_O represented the hypothesis that chick survival was not a function of year. Models S_{Y+m} and S_m incorporated daily chick

masses as an individual covariate. Model S_{Y+m} represented the hypothesis that chick survival was a function of both year and chick mass. Model S_m represented the hypothesis that chick survival was a function of chick mass but not of year. Again, the best model was identified based on AIC_C model selection. This best model was used to estimate the probability of the chicks surviving until the end of the study.

RESULTS

Forb Abundance

The forb abundances of the exposure sites were not all within the nominal category range due to changes in forb abundance over time and inaccurate preliminary estimation. The extent of these discrepancies was indicated by mean forb abundances and their 95% confidence intervals (Table 2.3 and Fig. 2.1). The data from the first and second months of 2003 was presented separately to allow comparison with 2002, which only lasted 1 month.

Arthropod abundance

No relationship was found between forb abundance and the mean total invertebrate abundance or invertebrate order richness. Of the 15 orders of invertebrates collected, the only order whose abundance was shown to be related to forb abundance was Coleoptera, which increased with forb abundance (Geelhood 2003).

Mass

The average daily mass of the chicks in each group was plotted to illustrate the growth curves of the chicks in 2002 and 2003 (Fig. 2.2). There was no evidence that forb abundance in the exposure areas had an effect on the mass gain rate of chicks in 2002. The model with no treatment effect (R_o) had an Akaike weight of 0.97 while the model with a treatment effect (R_F) had an Akaike weight of only 0.02 (Table 2.4). Standard diagnostics did not indicate any

violations of the assumptions of the model. Fig. 2.3 indicates that Model R_{o} adequately fit the data.

In contrast, there was strong evidence that mass gain rate of chicks increase with forb abundance in 2003. Model R_F was the best model (Table 2.4) receiving 0.82 of the Akaike weight. In addition, the combined Akaike weight of the 2 models with a forb effect was 1.00. Gender was not an important covariate in this analysis. Standard diagnostics did not indicate any violations of the assumptions of the model. Fig. 2.4 indicates that Model R_F adequately fit the data. The plot of the predicted masses over time from model R_F of each treatment group (Fig. 2.8) shows that the chicks exposed to high-forb-abundance areas gained mass at a faster rate than those exposed to medium-forb-abundances areas followed by chicks exposed to low-forb-abundance areas.

There was very strong evidence that the mass gain rate in 2003 was greater than that in 2002, with model $R_{\rm Y}$ receiving much more support than model $R_{\rm o}$. Standard diagnostics did not indicate any violations of the assumptions of the model. Fig. 2.6 indicates that Model $R_{\rm Y}$ adequately fit the data. The plot of the predicted masses over time for each year shows that the chicks grew more rapidly in 2003 than 2002 (Fig. 2.7).

Feather Growth

The average daily feather length of the chicks in each group was plotted to illustrate the growth curves of the chicks in the 3 groups (Fig. 2.8). There was no evidence that forb abundance in the exposure areas had an effect on the feather growth rate of chicks in 2002. The model with no treatment effect (R_o) had an Akaike weight of 0.998 while the model with a treatment effect (R_F) had an Akaike weight of only 0.002 (Table 2.5). Standard diagnostics did not indicate any violations of the assumptions of the model. Fig. 2.9 indicates that Model R_o adequately fit the data.

In contrast, there was strong evidence that feather growth rate of chicks increase with forb abundance in 2003. Model R_{FG} , which had both a treatment and a gender effect, was the best model (Table 2.5) receiving 0.82 of the Akaike weight. In addition, the combined Akaike weight of the 2 models that included a forb effect (i.e., R_{FG} and R_F) was 0.98. Standard diagnostics did not indicate any violations of the assumptions of the model. Fig. 2.10 indicates that Model R_{FG} adequately fit the data. The plot of the predicted feather length over time from model R_{FG} of each treatment group shows that the chicks exposed to high-forb-abundance areas grew at a faster rate than those exposed to medium-forb-abundances areas followed by chicks exposed to low-forb-abundance areas (Fig. 2.11). The predictions for the males and females have been presented separately to improve the interpretability of the plots. Gender was an important covariate with a combined Akaike weight of the 2 models that contained gender effect of 0.83. Males grew at a faster rate than females (Fig. 2.12).

There was evidence that the feather growth rates in 2003 were higher than in 2002, with model $R_{\rm Y}$ receiving 0.88 of the Akaike weight. Standard diagnostics did not indicate any violations of the assumptions of the model. Fig. 2.13 indicates that Model $R_{\rm Y}$ adequately fit the data. The plot of the predicted feather lengths over time of for each year shows that the chicks grew more rapidly in 2003 than 2002 (Fig. 2.14).

Survival

As expected, the data did not support the hypothesis that the forb abundance in exposure areas affected chick survival in 2002 or 2003. The combined Akaike weights of the models with no forb abundance effect (i.e., S_m and S_o) were 0.85 in 2002 and 0.54 in 2003. The combined Akaike weights of the models with a forb abundance effect (i.e., S_{fa} and S_{fa+m}) were 0.15 and 0.46 (Table 2.6). The estimated probability of chick survival to 27 days in 2002 from the best model (S_m) was 0.39 (95% CI = 0.21 to 0.61). The estimated probability of chick survival to 54 days in 2003 from the best model (S_m) was 0.79 (95% CI = 0.64 to 0.89).

There was strong evidence that chick survival to 27 days was higher in 2003 than in 2002. The combined weight of the models with a year effect (i.e., S_Y and S_{Y+m}) was 0.99, while the combined Akaike weight of the models with no year effect (i.e., S_O and S_m) was 0.01 (Table 2.6). The estimated probabilities of chick survival to 27 days from the best model (S_{Y+m}) were 0.35 (95% CI = 0.17 - 0.59) and 0.78 (95% CI = 0.63 - 0.88) in 2002 and 2003, respectively.

DISCUSSION

In 2002, contrary to expectations, there was no evidence for an effect of forb abundance on either the mass gain rate or feather growth rate of chicks. In contrast, both response variables were found to increase with forb abundance in 2003. Assuming that the protein content of forage in brood areas increases with forb abundance, the 2003 result agrees with Johnson and Boyce (1990) and Jorgensen and Blix (1985), who showed that the mass gain rate of captive sage-grouse and willow ptarmigan chicks, respectively, increased with the protein content of the food offered to them.

There were several differences between the 2002 and 2003 studies that could have led to the conflicting results. These differences included location, climate, and chick source population. More important may have been the design changes made after the experiments in 2002. These changes included exposing chicks to sagebrush habitat at a younger age, increasing the duration of the study, increasing the chicks' daily feeding opportunity, decreasing the daily distances traveled by the chicks during feeding, and increasing sample size. Differences between the 2 years resulted in higher chick survival, higher mass gain rate and higher feather growth rate in 2003 than in 2002.

Mass gain was a better response variable than feather growth in that it demonstrated greater difference between treatment groups. In addition, mass measurements required less time, less handling of the birds, were more accurate and varied less between observers than feather

measurements. In addition, feather measurements became unreliable to impossible when feathers were damaged, lost or molted.

The data provided no evidence that forb abundance affected chick survival in either year. This result was expected, given that the study was not designed to investigate survival and that interventions were made to prevent mortality. Previous studies have shown correlation between chick growth rates and survival rates. Johnson and Boyce (1990) and Jorgenson and Blix (1985) reported that both the growth and survival of captive sage-grouse and willow ptarmigan chicks, respectively, decreased with the amount of invertebrates in the diet. In addition, studies on wild chicks have found correlations between growth rate and survival in willow ptarmigan (Myrberget 1977), mallards (*Anas platyrhynchos*) (Cox et al. 1998) and red grouse (*Lagopus lagopus scoticus*) (Park et al. 2001). Similarly, Stokes (1954) found that pheasant chicks that were below the mean mass in the fall were recovered at a lower rate during the hunting season, presumably due to increased mortality. These results, combined with those of the current study, supports the hypothesis by Drut et al. (1994b) that reduced forb abundance may lead to reduced sage-grouse productivity via reduced chick growth and survival.

Forb abundance in upland sagebrush habitat during the brood period is very dynamic, capable of changing rapidly in response to temperature and precipitation. As a result, it was difficult to procure suitable exposure sites. Sites that were estimated to have medium-forb-abundance during the evaluation visit were found to have shifted to either the high or low-forb-abundance 3 days later when the chicks were exposed to the site. Consequently, chicks were sometimes exposed to sites with an actual forb abundance that was not within the nominal treatment range. Table 2.3 reveals that these anomalies were not severe. The mean forb abundances and their 95% confidence intervals show that greater separation was achieved between the treatment levels in 2003 than in 2002.

Individual chicks were considered the experimental units in this study. The analyses used assume independence between the experimental units. The response of a chick, in terms of

growth, to forb abundance of brood habitats is affected by their genotypic and phenotypic characteristics as well as environmental influences. Balancing nest mates across treatment groups maximized the genotypic and phenotypic independence of chicks within each treatment group. However, the chicks within a treatment group were transported together, remained together as a brood during field exposures and interacted with each other during exposures; this resulted in a failure to fully meet the assumption of independence. The result is an underestimation of the variances within groups to an unknown degree (Burnham et al. 1987).

RESEARCH NEEDS

There has been much research on sage-grouse / habitat relationships. This research has formed the basis for hypotheses on a number of grouse-habitat relationships. Experiments need to be conducted to evaluate these hypotheses and to firmly establish, quantify and determine the mechanism behind the relationships.

This study has shown that, at least in some years, chick growth rates increase with forb abundance in brood areas. More information is needed on the shape of the response function in order to determine the benefits of increasing forb abundance over a range of base levels. In addition, the relationship between forb abundance and chick growth, needs to be confirmed over a wider geographic and climactic range. Future studies could examine the effect of forb abundance in brood habitat on the long-term survival of chicks and the role of specific forb species. More information is also needed on the role of sagebrush and rabbitbrush in brood habitats in chick nutrition.

Invertebrates form an important component of the sage-grouse chick's diet for up to 3 months of age. More information is needed on the role of invertebrates in brood areas. What is the relationship between invertebrate abundance and chick growth and survival? Which invertebrate species are used by the chicks and which are not? Which invertebrates are available to the chicks and when are they available? Experiments conducted to explore the relationship

between invertebrates in brood areas and chick growth and survival will require the development of entomological sampling techniques that account for invertebrate availability to and use by sage-grouse chicks. In order to manage the invertebrate community of brood areas, more information is needed on the association between the vegetation and invertebrates of brood habitat. For example, can increasing the abundance of certain plants benefit chicks by increasing the abundance of invertebrate species that are eaten by chicks?

MANAGEMENT IMPLICATIONS

This study showed that chick growth rates increase as forb abundance in brood areas increases from <10 to >20%. This result in combination with previous studies that have found a correlation between growth rates and survival suggests that management actions that increase forb abundance in brood areas with <20% forb abundance may lead to increased chick survival and grouse productivity.

Chapter 2 contains a list of forbs directly consumed by chicks. A selection of these forbs appropriate the area under consideration should be included in seed mixes used to reseed brood areas. Invertebrates are a very important food source for chicks. Forbs and shrubs that support invertebrate populations should also be included in seed mixes.

The chicks in this study used sagebrush in several ways. First, they gleaned aphids, ants, cicadas and other invertebrate species from the leaves and stems of sagebrush. During certain times, these invertebrates made up a large portion of the chicks' diet (see Chapter 2). Secondly, after 3 weeks of age, the chicks consumed the sagebrush leaves, seemingly preferring to feed on young plants and new growth. Thirdly, the chicks used the sagebrush structure for thermal cover and for predator avoidance. Management actions to improve sage-grouse habitat should, therefore, retain sagebrush of various ages and heights.

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Table 2.1: Structure of models used to evaluate the effects of forb abundance and year on the mass and feather growth of human-imprinted sage-grouse chicks in Middle Park and Moffat County Colorado in 2002 and 2003, respectively. In these models t is time, G is gender, H is the high-forb-abundance treatment, L is the low-forb-abundance treatment, L is the error term. The response variables were the empirical growth rates $\left(\frac{M_{i+1}-M_i}{t_{i+1}-t_i}\right)$ and $\frac{F_{i+1}-F_i}{t_{i+1}-t_i}$,

where M_i is the chick mass at time i, F_i is the length of the 7th primary feather at time i, and t_i is the days since hatch at time i. K is the number of parameters estimated by each model.

Model	Structure	K				
Effect of Forb Abundance on Growth						
R_{o}	$\beta_1 + 2\beta_2 t + 3\beta_3 t^2 + e_i$	5				
R_{F}	$\beta_1 + 2\beta_2 t + 3\beta_3 t^2 + \beta_4 H + 2\beta_5 H t + 3\beta_6 H t^2 + \beta_7 L + 2\beta_8 L t + 3\beta_9 L t^2 + e_i$	11				
R_{G}	$\beta_1 + 2\beta_2 t + 3\beta_3 t^2 + \beta_4 G + 2\beta_5 G t + 3\beta_6 G t^2 + e_i$	8				
R_{FG}	$\beta_{1}+2\beta_{2}t+3\beta_{3}t^{2}+\beta_{4}G+2\beta_{5}Gt+3\beta_{6}Gt^{2}+\beta_{7}H+2\beta_{8}Ht+3\beta_{9}Ht^{2}\\+\beta_{10}L+2\beta_{11}Lt+3\beta_{12}Lt^{2}+e_{i}$	14				
Effect of Ye	ear on Growth					
R_{o}	$\beta_1 + 2\beta_2 t + 3\beta_3 t^2 + e_i$	5				
R_{Y}	$\beta_1 + 2\beta_2 t + 3\beta_3 t^2 + \beta_4 Y + 2\beta_5 Y t + 3\beta_6 Y t^2 + e_i$	8				

Table 2.2: Models used to evaluate the effects of forb abundance and year on the survival of human-imprinted sagegrouse chicks in Middle Park and Moffat County Colorado in 2002 and 2003, respectively. K is the number of parameters estimated by each model.

Model	Effects	K
Effect of Forb	Abundance on Survival	
S_{o}	None	1
S_{fa}	Forb abundance	3
S_{m}	Mass	2
S_{fa+m}	Forb abundance and mass	4
Effect of Year	on Survival	
S_o	None	1
S_{Y}	Year	2
S_{m}	Mass	2
S_{Y+m}	Year and mass	3

Table 2.3: Forb abundance of low, medium, and high-forb-abundance exposure sites in Middle Park and Moffat County, Colorado in 2002 and 2003, respectively. Shown are the mean forb abundance and associated 95% CI and the range of forb abundance in each category in 2002 field season and the first month, the second month and totals in 2003.

Category	n	Mean (%)	959	% CI	Ra	nge
2002 (5/27 – 6/22)				13187		
Low	6	8	5	12	5	13
Med	6	12	8	17	7	21
High	6	27	19	35	19	45
2003 Month 1 (5/2	2 - 6/1	7)				
Low	9	9	7	12	3	13
Med	9	17	13	21	13	22
High	9	27	20	34	18	41
2003 Month 2 (6/1	8 - 7/1	14)				
Low	9	3	1	4	1	6
Med	9	10	7	14	4	16
High	9	19	15	23	14	29
2003 Total (5/22 -	7/14)					
Low	18	6	5	7	1	13
Med	18	14	11	16	4	22
High	18	23	19	27	14	41

Table 2.4: Model selection results for the effect of forb abundance and year on mass gain rates (g/d) of human-imprinted sage-grouse chicks in Middle Park and Moffat County, Colorado in 2002 and 2003, respectively.

Mo	del	n	K	log (L)	AICc	Δ	w_i^a
Forb a	bundanc	ee 2002					
	R_{o}	162	5	-402.2	814.7	0.0	0.97
	$R_{\rm F}$	162	11	-399.4	822.5	7.8	0.02
Forb a	bundanc	ee 2003					
	$R_{\rm F}$	1476	11	2968.6	-5914.9	0.0	0.82
	R_{FG}	1476	14	2970.1	-5911.9	3.0	0.18
	R _o	1476	5	2951.8	-5893.5	21.5	0.00
	R_G	1476	8	2953.8	-5891.5	23.4	0.00
Year							
	$R_{\rm Y}$	918	8	1811.3	-3606.3	0.0	1.00
	Ro	918	5	1773.9	-3537.7	68.6	0.00

 $^{^{}a}w_{i}$ is the probability that model *i* is the best model of those considered.

Table 2.5: Model selection results for the effect of forb abundance and year on feather growth rates (mm/d) of human-imprinted sage-grouse chicks in Middle Park and Moffat County, Colorado in 2002 and 2003, respectively.

Model		n	K	log (L)	AICc	Δ	w_i^{a}
Forb ab	undan	ce 2002	TH				
	R _o	156	5	-358.4	727.1	0.0	0.998
	R_{F}	156	11	-357.9	739.6	12.5	0.002
Forb ab	undan	ce 2003					
	R_{FG}	351	14	-469.3	967.9	0.0	0.82
	R_{F}	351	11	-474.2	971.2	3.3	0.16
	R_G	351	8	-479.9	976.1	8.3	0.01
	R _o	351	5	-483.3	976.7	8.8	0.01
Year							
	R_{Y}	378	8	-737.5	1491.3	0.0	0.88
	R _o	378	5	-742.6	1495.3	4.0	0.12

 $^{{}^{}a}w_{i}$ is the probability that model i is the best model of those considered.

Table 2.6: Model selection results for known fate models of the effect of forb abundance, mass and year on the survival of human-imprinted sage-grouse chicks in Middle Park and Moffat County, Colorado in 2002 and 2003, respectively.

Mode	el	K	AICc	Δ	w_i^{a}
Forb a	abundance	and mass 200	2		
	S_{m}	2	97.30	0.00	0.83
	S_{fa+m}	4	100.85	3.54	0.14
	S_o	1	104.83	7.53	0.02
	S_{fa}	3	106.94	9.64	0.01
Forb a	abundance	and mass 200	3		
	S_{m}	2	109.55	0.00	0.49
	S_{fa+m}	4	109.93	0.38	0.41
	S_{fa}	3	113.96	4.41	0.05
	S_o	1	114.47	4.92	0.04
Year					
	S_{Y+m}	3	206.86	0.00	0.71
	S_{m}	2	208.69	1.83	0.28
	S_{Y}	2	215.45	8.58	0.01
	S_{o}	1	222.11	15.24	0.00

 $^{^{}a}w_{i}$ is the probability that model i is the best model of those considered.

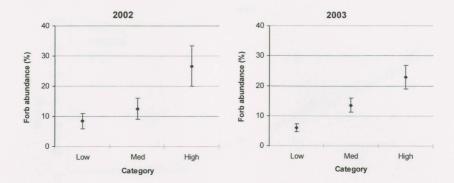


Fig. 2.1: Mean forb abundance present at low, medium, and high-forb-abundance exposure sites in Middle Park and Moffat County, Colorado in 2002 and 2003, respectively; error bars represent 95% CI's.

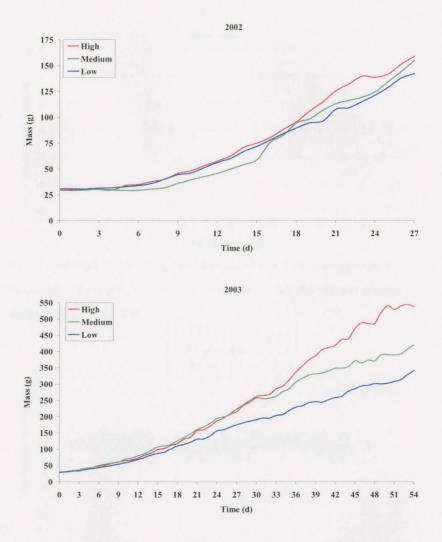


Fig. 2.2: Average daily masses of human-imprinted sage-grouse in low, medium, and high treatment groups in Middle Park and Moffat County, Colorado in 2002 and 2003, respectively.

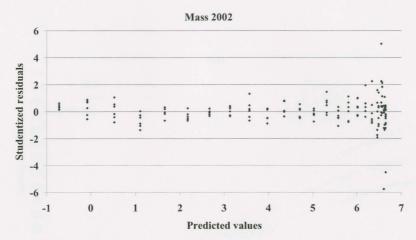


Fig. 2.3: Studentized residuals versus predicted values from model R_o of the mass gain of human-imprinted sage-grouse chicks exposed to low, medium, and high treatment groups in Middle Park, Colorado in 2002.

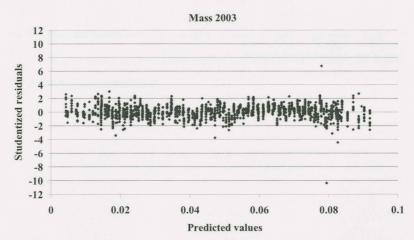


Fig. 2.4: Studentized residuals versus predicted values from model R_{F} of the mass gain of human-imprinted sage-grouse chicks exposed to low, medium, and high treatment groups in Moffat County, Colorado in 2003.

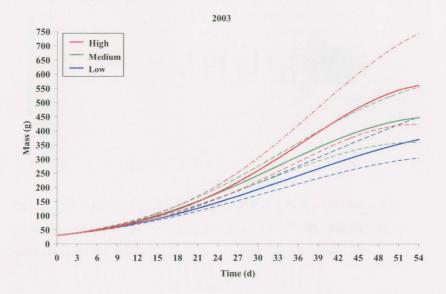


Fig. 2.5: Predicted growth curves from model R_F of human-imprinted sage-grouse chicks exposed to high, medium, and low-forb abundance brood areas of Moffat County, CO in 2003. The dashed lines represent 95% CI's.

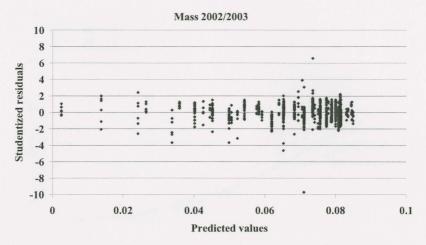


Fig. 2.6: Studentized residuals versus predicted values from model R_{Υ} of the mass gain of human-imprinted sage-grouse chicks exposed to low, medium, and high treatment groups in brood areas of Middle Park and Moffat County, CO in 2002 and 2003, respectively.

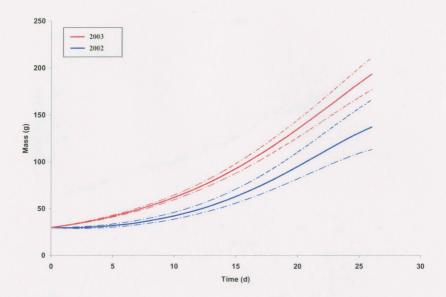


Fig. 2.7: Predicted mass gain from model $R_{\rm Y}$ of human-imprinted sage-grouse chicks exposed to brood areas of Middle Park and Moffat County, CO in 2002 and 2003, respectively. The dashed lines represent 95% CI's.

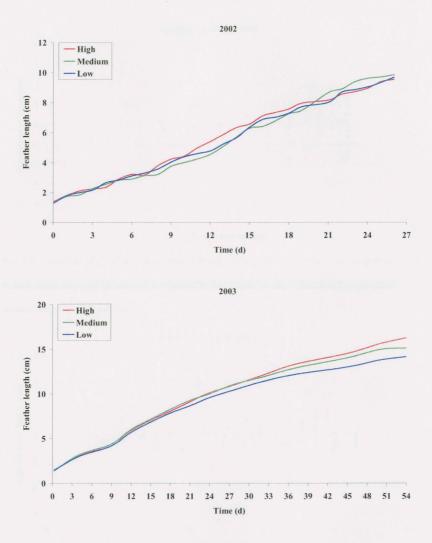


Fig. 2.8: Average daily feather lengths of human-imprinted sage-grouse in low, medium, and high treatment groups in Middle Park and Moffat County, Colorado in 2002 and 2003, respectively.

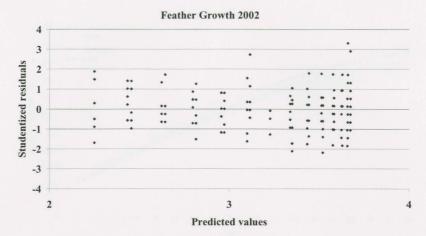


Fig. 2.9: Studentized residuals versus predicted values from model R_o of the feather growth of human-imprinted sage-grouse chicks exposed to low, medium, and high treatment groups in Middle Park, Colorado in 2002.

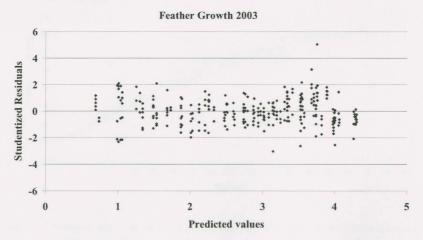
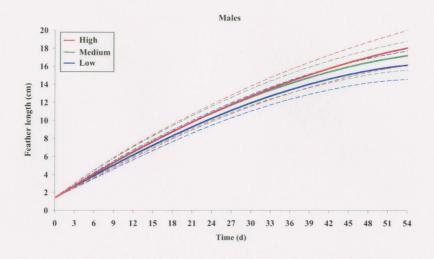


Fig. 2.10: Studentized residuals versus predicted values from model R_{FG} of the feather growth of human-imprinted sage-grouse chicks exposed to low, medium, and high treatment groups in Moffat County, Colorado in 2003.



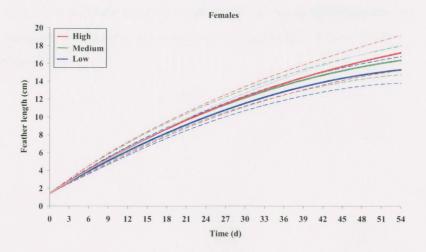


Fig. 2.11: Predicted feather growth curves from model R_{FG} of male and female human-imprinted sage-grouse chicks exposed to high, medium, and low-forb abundance brood areas of Moffat County, CO in 2003. The dashed lines represent 95% CI's.

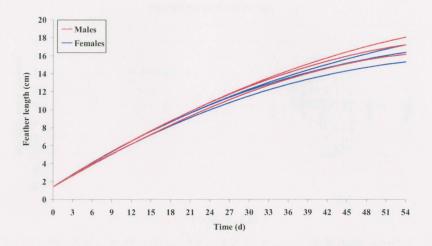


Fig. 2.12: Predicted feather growth curves from model R_{FG} of male and female human-imprinted sage-grouse chicks exposed to high, medium, and low-forb abundance brood areas of Moffat County, CO in 2003.

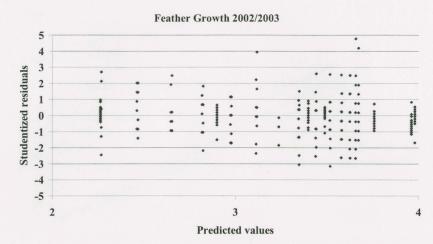


Fig. 2.13: Studentized residuals versus predicted values from model $R_{\rm Y}$ of the feather growth of human-imprinted sage-grouse chicks exposed to low, medium, and high treatment groups in brood areas of Middle Park and Moffat County, CO in 2002 and 2003, respectively

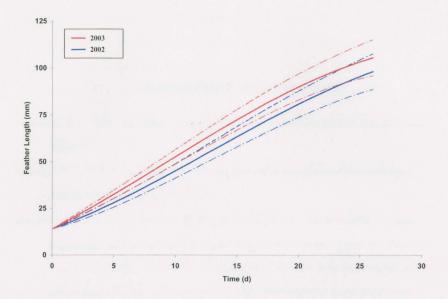


Fig. 2.14: Predicted feather growth curves from model R_Y of human-imprinted sage-grouse chicks exposed to brood areas of Middle Park and Moffat County, CO in 2002 and 2003, respectively. The dashed lines represent 95% CI's.

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APPENDIX

APPENDIX

Data on the physical properties, collection, storage, incubation and hatch of sage-grouse eggs collected from wild hens and used in studies on human-imprinted sage-grouse in Middle Park and Moffat Count, Colorado in 2002 and 2003, respectively.

V	E	11	Collection	Days	II-t-l	Collection	Incubation	Length	Width
Year	Egg	Hen	date	stored	Hatch	mass (g)	loss (%)	(cm)	(cm)
2002	1	7	4/18	9	yes	43.2	12	5.5	3.8
2002	2	7	4/18	9	yes	41.8	12	5.5	3.6
2002	3	7	4/18	9	yes	42.1	13	5.4	3.6
2002	4	7	4/18	9	yes	37.3	13	5.1	3.6
2002	5	3	4/20	7	yes	48.8	12	5.9	3.8
2002	6	6	4/20	7	yes	47.9	12	5.6	3.9
2002	7	6	4/20	7	yes	45.1	11	5.5	3.8
2002	8	6	4/22	5	yes	47.4	11	5.6	3.9
2002	9	6	4/22	5	yes	45.3	13	5.6	3.8
2002	10	3	4/22	5	yes	47.0	13	5.6	4.0
2002	11	3	4/22	5	yes	44.3	13	5.9	3.8
2002	12	5	4/23	4	yes	44.8	11	5.7	4.0
2002	13	5	4/23	4	yes	44.9	12	5.8	4.0
2002	14	5	4/23	4	yes	46.8	11	6.3	3.8
2002	15	3	4/23	4	yes	48.1	12	5.9	3.8
2002	16	5	4/24	3	yes	47.0	11	5.9	3.8
2002	17	5	4/24	3	no	43.6	13	5.8	3.7
2002	18	6	4/24	3	yes	45.8	10	5.5	3.8
2002	19	4	4/24	3	yes	48.7	11	5.5	3.9
2002	20	4	4/24	3	no	49.8	10	5.6	4.0
2002	21	4	4/24	3	yes	46.7	10	5.5	3.9
2002	22	4	4/24	3	yes	49.1	12	5.6	4.1
2002	23	4	4/24	3	yes	44.1	11	5.5	3.8
2002	24	4	4/24	3	no	47.7	9	5.6	3.9
2002	25	4	4/24	3	yes	47.4	11	5.6	3.9
2002	26	5	4/25	2	no	44.6	11	5.6	3.8
2002	27	1	4/25	2	no	45.3	14	5.6	3.8
2002	28	1	4/25	2	yes	46.4	14	5.8	3.8
2002	29	1	4/25	2	yes	45.5	15	5.6	3.8
2002	30	1	4/25	2	yes	45.6	13	5.6	3.8
2002	31	1	4/25	2	yes	45.0	14	5.6	3.7
2002	32	1	4/25	2	yes	43.1	15	5.5	3.7
2002	33	8	4/23	4	no	46.9		5.5	4.0
2002	34	2	4/26	1	no	44.3		5.4	3.8
2002	35	2	4/26	1	yes	43.0	12	5.5	3.8
2002	36	2	4/26	1	yes	42.3	13	5.5	3.7
2002	37	2	4/26	1	yes	39.2	13	5.4	3.5
2002	38	2	4/26	1	yes	42.9	12	5.5	3.7
2002	39	5	4/26	1	yes	44.4	12	5.6	3.8
2002	40	3	4/26	1	ves	48.6	12	5.9	3.8

Year	Egg	Hen	Collection date	Days stored	Hatch	Collection mass (g)	Incubation loss (%)	Length (cm)	Widt (cm)
2002	41	3	4/26	1	yes	47.5	13	5.8	3.8
2002	42	6	4/26	1	yes	46.9	12	5.5	3.9
2002	43	1	4/27	0	no	45.8	13	5.6	3.8
2002	44	3	4/27	0	yes	46.0	13	5.8	3.8
2003	7	87	4/13	11	no	48.4	11	5.9	3.9
2003	8	87	4/13	11	no	46.4	12	5.6	3.8
2003	9	87	4/13	11	yes	47.0	12	5.7	3.9
2003	10	87	4/13	11	yes	46.4	11	5.5	3.9
2003	11	87	4/13	11	no	48.3	14	5.6	3.9
2003	12	87	4/13	11	yes	45.1	13	5.6	3.8
2003	13	87	4/13	11	-	47.4	11	5.6	3.9
				10	yes	43.5	14	5.5	3.7
2003	14	87	4/14		yes		13	5.6	3.7
2003	15	91	4/14	10	yes	42.5	15		
2003	16	91	4/14	10	yes	43.3	15	5.6	3.7
2003	17	91	4/14	10	yes	43.4		5.8	3.7
2003	18	91	4/14	10	no	45.2		6.0	3.7
2003	19	91	4/14	10	yes	44.4	14	5.7	3.7
2003	20	91	4/14	10	no	42.2		6.0	3.6
2003	21	91	4/14	10	no	44.0	13	5.7	3.7
2003	22	91	4/14	10	no	44.6		5.8	3.7
2003	23	91	4/14	10	yes	43.3	13	5.6	3.7
2003	24	70	4/14	10	no	43.9		5.6	3.8
2003	25	70	4/14	10	no	43.5		5.5	3.8
2003	26	70	4/14	10	no	44.0		5.6	3.8
2003	27	70	4/14	10	no	45.6		5.6	3.8
2003	28	70	4/14	10	yes	39.9	14	5.2	3.7
2003	29	70	4/14	10	no	44.5		5.5	3.8
2003	30	70	4/14	10	no	45.3		5.6	3.8
2003	31	70	4/14	10	no	43.4		5.4	3.7
2003	32	70	4/14	10	no	40.4		5.5	3.7
2003	33	92	4/14	10	yes	44.5	13	5.2	3.9
2003	34	92	4/14	10	yes	46.1	13	5.3	4.0
2003	35	92	4/14	10	yes	47.2	12	5.3	3.9
2003	36	92	4/14	10	yes	44.7	12	5.2	3.9
2003	37	92	4/14	10	yes	42.6	14	5.2	3.8
2003	38	92	4/14	10	yes	47.9	11	5.4	4.0
2003	39	92	4/14	10	yes	46.6	12	5.3	4.0
2003	40	96	4/14	10	yes	45.7	13	5.6	3.8
2003	41	96	4/14	10	yes	46.6	14	5.6	3.9
2003	42	96	4/14	10	yes	43.0	15	5.6	3.8
	43	96	4/14	10		45.4	14	5.7	3.8
2003					yes		14	5.7	
2003	44	96	4/14	10	yes	45.3			3.8
2003	45	96	4/14	10	yes	48.4	15	5.6	4.0
2003	46	91	4/15	9	no	42.0	4.4	5.6	3.7
2003	47	94	4/15	9	yes	43.8	14	5.4	3.8
2003	48	94	4/15	9	yes	44.7	16	5.6	3.8
2003	49	94	4/15	9	yes	43.0	14	5.7	3.7
2003	50	94	4/15	9	yes	46.4	14	5.6	3.7

Year	Egg	Hen	Collection date	Days stored	Hatch	Collection mass (g)	Incubation loss (%)	Length (cm)	Width (cm)
2003	51	94	4/15	9	yes	44.1	15	5.6	3.8
2003	52	94	4/15	9	yes	46.0	15	5.6	3.8
2003	53	94	4/15	9	yes	45.3	15	5.7	3.8
2003	54	92	4/16	8	yes	45.8	12	5.2	3.9
2003	55	96	4/16	8	no	45.0		5.6	3.7
2003	56	71	4/16	8	yes	44.6	13	5.7	3.7
2003	57	71	4/16	8	yes	45.8	13	6.0	3.8
2003	58	71	4/16	8	no	43.7	13	5.8	3.7
2003	59	71	4/16	8	no	43.8	13	5.7	3.7
2003	60	71	4/16	8	yes	42.2	14	5.4	3.7
2003	61	71	4/16	8	yes	44.8	14	5.6	3.8
2003	62	71	4/16	8	yes	44.8	13	5.8	3.8
2003	63	71	4/16	8	no	44.3	14	5.8	3.7
2003	64	71	4/16	8	no	45.2	12	5.7	3.8
2003	65	81	4/17	7	no	41.0	13	5.4	3.7
2003	66	81	4/17	7	yes	39.1	15	5.3	3.7
2003	67	81	4/17	7	yes	39.3	15	5.3	3.7
2003	68	81	4/17	7	yes	39.8	15	5.2	3.7
2003	69	92	4/17	7	yes	46.7	12	5.4	4.0
2003	70	94	4/17	7	yes	42.2	14	5.4	3.6
2003	71	81	4/18	6	yes	39.6	14	5.2	3.6
2003	72	94	4/18	6	yes	40.0	16	5.4	3.7
2003	73	81	4/21	3	yes	41.1	13	5.4	3.7
2003	74	81	4/21	3	yes	39.9	13	5.2	3.7



