

THE UNIVERSITY OF CALGARY

Body Mass Variation in Breeding Mountain Bluebirds (Sialia currucoides):  
Effect of Stress or Adaptation for Flight?

by

Marilyn Susan Merkle

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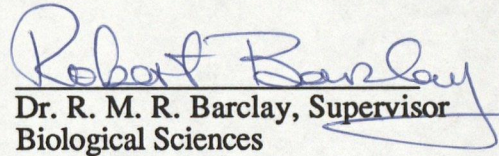
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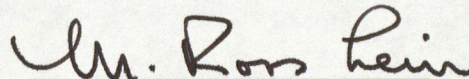


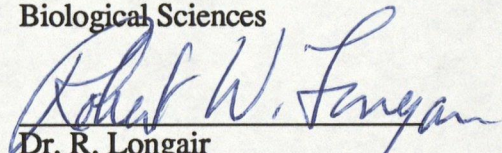


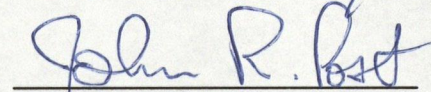
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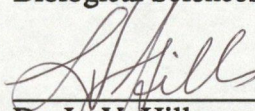
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## **ABSTRACT**

I examined body mass changes of Mountain Bluebirds (Sialia currucoides) in two different years using a perch connected to a portable electronic balance. Females gained mass prior to egg laying and incubation. Mass loss began during incubation and continued into the nestling period. Males maintained mass throughout the nesting cycle. Females were heavier than males during laying and incubation but had the same mass as males by the end of the nesting cycle. In a food supplementation experiment, supplemented birds lost mass in the same pattern as control birds, except during the early nestling period. Results support the flight adaptation hypothesis for mass loss. Females put on mass before incubation and use this energy reserve when foraging conditions are unfavourable. Extra mass is lost when conditions become more favourable, decreasing flight costs and increasing flight performance. Males maintain a low body mass because they are not constrained by incubation.



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For my dad  
for taking an interest in all things wild

and

For Kicha  
The Crazy-Spirited One

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## INTRODUCTION

Life history theory is based on the assumption that trade-offs exist between various activities in the life of an iteroparous organism (Stearns 1976; Reznick 1985; Hochachka 1992). One such trade-off involves the cost of reproduction where increased fecundity or parental investment causes a decrease in longevity or a reduced capacity for future reproduction (Reznick 1985; Orell and Koivula 1988). Natural selection should favour individuals that maximize the net benefits of reproduction. Costs of reproduction may include loss of physiological condition or an enhanced risk of predation (Johnson et al. 1990), while the benefits of reproduction include higher lifetime fitness. Patterns of body mass change in breeding birds frequently have been viewed as evidence for the presence or absence of reproductive stress (Moreno 1989a). Mass loss, in particular, has been used as an index of reproductive costs in several studies of avian life history (Askenmo 1977; Bryant 1979; De Steven 1980; Westerterp et al. 1982; Nur 1984a,b; Dijkstra et al. 1990; Johnson et al. 1990). However, patterns of mass change may not be a consequence of reproductive stress, but an outcome of adaptive compromises among different selective factors (Moreno 1989a). Thus, it is important to understand the patterns and the causes of body mass change because body mass variation appears to be a consistent component of avian life history strategies.

Body mass frequently varies in passerines, often in relation to environmental and physiological factors (Biermann and Sealy 1985). During the breeding season, females of many species gain body mass prior to egg laying, maintain mass during the incubation period, and lose mass while rearing young. Males show this pattern but to a lesser extent (see review in Ricklefs 1974; Table 1). Detailed information on body mass changes of individual birds during the breeding season is rare, and only a few studies have used repeated weighings of undisturbed birds (Crick and Fry 1986; Jones 1987a,b; Moreno 1989a,b). For this reason, hypotheses regarding the costs and benefits of mass variation

Table 1. Percent body mass loss throughout the breeding season in male and female passerines.

| SPECIES                     | SEX | % MASS<br>LOSS | REFERENCE                 |
|-----------------------------|-----|----------------|---------------------------|
| Bank Swallow                | F   | 18.8           | Petersen 1955             |
| <u>Riparia riparia</u>      | M   | 3.5            |                           |
|                             | F   | 13.9           | Jones 1987c               |
|                             | M   | 9.7            |                           |
| European Starling           | F   | 16.6           | Ricklefs and Hussell 1984 |
| <u>Sturnus vulgaris</u>     | M   | 5.2            |                           |
| Great Tit                   | F   | 6.6            | De Laet and Dhondt 1989   |
| <u>Parus major</u>          |     |                |                           |
| House Wren                  | F   | 12.5           | Freed 1981                |
| <u>Troglodytes aedon</u>    | M   | 1.8            |                           |
| Northern Wheatear           | F   | 11.8           | Moreno 1989b              |
| <u>Oenanthe oenanthe</u>    | M   | 11.0           |                           |
| Pied Flycatcher             | F   | 20.0           | Silverin 1981             |
| <u>Ficedula hypoleuca</u>   | M   | 3.2            |                           |
| Red Throated Bee-eater      | F   | 13.6           | Crick and Fry 1986        |
| <u>Merops bullocki</u>      | M   | 6.5            |                           |
| Tree Swallow                | F   | 14.6           | Williams 1988             |
| <u>Tachycineta bicolor</u>  |     |                |                           |
| Wood Thrush                 | F   | 11.0           | Johnson et al. 1990       |
| <u>Hylocichla mustelina</u> |     |                |                           |
| Yellow-rumped Cacique       | F   | 13.3           | Robinson 1986             |
| <u>Cacicus cela</u>         |     |                |                           |
| Yellow Warbler              | F   | 12.3           | Biermann and Sealy 1985   |
| <u>Dendroica petechia</u>   | M   | 5.0            |                           |

throughout the breeding season have not been tested adequately. The reduction in mass during the nestling period may be especially important because energy demands on the parents are at a peak (Bryant and Westerterp 1983; Moreno and Hillstrom 1992), with some parents making up to 500 feeding trips per day (Norberg 1981). In addition, most of the mass loss seems to occur at this time (Hussell 1972; Bryant 1979; Drent and Daan 1980; Freed 1981; Westerterp et al. 1982; Newton et al. 1983; Ricklefs and Hussell 1984; Crick and Fry 1986; Jones 1986; Moreno 1989a; Dijkstra et al. 1990).

There are several hypotheses regarding body mass loss during the breeding season. Mass loss may be due to atrophy of the reproductive organs following copulation, egg formation and laying (Petersen 1955; Ricklefs 1974; Silverin 1975; Krementz and Ankney 1988; Johnson et al. 1990). If this is the case, then it might be expected that mass loss would occur early in incubation, immediately after egg laying. Indeed, in Pied Flycatcher (*Ficedula hypoleuca*) females, the ovary and oviduct atrophy within four days of egg laying (Silverin 1980). Similar results have been found in Bank Swallows (*Riparia riparia*; Petersen 1955; Bank Swallow and Sand Martin are the same species), Ring-necked Pheasants (*Phasianus colchicus*; Brietenbach and Meyer 1959), White-crowned Sparrows (*Zonotrichia leucophrys*; King et al. 1966), and Swallows (*Hirundo rustica*; Jones 1987c; Swallow and Barn Swallow are the same species). Other carcass analyses have shown that in some species, reproductive organs are fully atrophied by the end of incubation (Silverin 1978; Ricklefs and Hussell 1984; Jones 1987c). However, most of the body mass loss occurs late in the nesting cycle, during the nestling period (Freed 1981; Crick and Fry 1986; Jones 1986; Moreno 1989b). Thus, atrophy of the gonads may only account for a small portion of the mass changes seen.

The gonadal atrophy hypothesis is also not supported by the fact that at the height of the nesting cycle the reproductive organs weigh relatively little. In American Robins (*Turdus migratorius*), for example, the testes weigh  $807 \pm 26$  mg and the ovaries weigh  $812 \pm 223$  mg at copulation and egg laying (Kemper and Taylor 1981). For a bird

that normally weighs 77 g (Dunning 1984), regression of the reproductive organs would represent only approximately one percent of the total body mass. If American Robins, like other passerines, experience a 10 to 15 % change in body mass over the entire breeding season, this would only explain a small portion of the total change in body mass. Similar relationships between gonad weight and body mass were seen in Black-billed Magpie males (Pica pica, one percent; Erpino 1969), White-crowned Sparrows (females, four percent, males, two percent, King et al. 1966; Lewis 1975), Great Tits (Parus major, females, two percent, males, one percent, Silverin 1978) and European Starling females (Sturnus vulgaris, five percent; Ricklefs and Hussell 1984). Thus, the gonads seem to weigh relatively little, even at the height of breeding, and their atrophy represents but a small portion of the total body mass loss, not enough to explain the total body mass variation, especially when much of the loss occurs during the nestling stage.

Others have hypothesized that mass loss while rearing young is evidence of physical stress. That is the nestlings place great energetic demands on their parents, who are thus forced to tap body fat reserves to meet these needs (see review in Ricklefs 1974; Askenmo 1977; Bryant and Westerterp 1980; Drent and Daan 1980; Yom Tov and Hilborn 1981; Robinson 1986; Hegner and Wingfield 1987; Moreno 1989b; Johnson et al. 1990). In other words, the inability to find food at a sufficient rate to maintain both young and parent creates a negative energy balance that leads to a reduction in body mass (Gaston and Jones 1989). The nestling period is a time of increased energy demands (Finch 1984; Martin 1987; Exo 1988), which may be twice those of other breeding stages, and may rise to 2.5 times when conditions are unfavourable (Bryant and Westerterp 1980). While rearing young, many birds fly faster, use more energetically-expensive search methods (Power 1980; Robinson 1986), fly farther (Robinson 1986) and/or increase the length of their working day (Kluijver 1950). In addition, adults of some species mobilize accumulated nutrient reserves during the nestling period as a response to higher feeding activity (Silverin 1981; Nur 1984a; Bryant 1988). In fact, a

positive correlation between nest visit rate and energy expenditure has been found (Bryant 1988), and mass loss is highly correlated with feeding frequency (Smith et al. 1988). If greater energy expenditure from a rising nest visitation rate leads to mass loss, this would reflect a decrease in body condition resulting from the allocation of limited resources to the offspring at the expense of self maintenance. Indeed, mass loss has often been used as an index for reproductive costs in birds (Askenmo 1977; Bryant 1979; De Steven 1980; Nur 1984a,b; Dijkstra et al. 1990). In addition, although not documented, mass loss may lead to greater mortality in that lighter birds may be more susceptible to starvation, parasites, and/or disease (Nur 1984b; Lima 1987; Bryant 1988). If the energetic demands of raising young are responsible for body mass loss in birds, mass loss should occur as the nestlings grow and should be greatest prior to fledging.

Body mass is lost prior to maximum food delivery in some birds including House Wrens (*Troglodytes aedon*; Freed 1981), European Starlings (Ricklefs and Hussell 1984), Sand Martins (Jones 1986), and Swallows (Jones 1987d). Body mass loss at this time does not fit the predictions for the reproductive stress hypothesis (Jones 1987d). An alternative hypothesis is that a decline in body mass in adults rearing young actually enhances parental fitness (Freed 1981; Norberg 1981). Flight is an energetically-costly form of locomotion (Utter and LeFebvre 1970; Bryant and Westerterp 1980; Drent and Daan 1980; Norberg 1981; Bryant 1988; Faaborg 1988), and a bird feeding nestlings expends a great deal of energy flying to and from the nest each hour (Bryant and Westerterp 1980; Drent and Daan 1980; Jones 1985 in Jones 1987b; Martin 1987; Bryant 1988; Weathers and Sullivan 1989). Any reduction in mass would increase flight performance and decrease flight costs, thus increasing the energy saved (Utter and LeFebvre 1970; Norberg 1981). The flight benefits of lower body mass include decreased wing loading (Croll et al. 1991), decreased aerodynamic drag, greater linear horizontal acceleration, greater horizontal flight speed, a faster rate of climb, and better angular roll acceleration and climbing ability (Norberg 1981; Jones 1986; Johnston



1990). These improvements in flight performance should be particularly important to birds that catch aerial prey such as insects. The energy saved through improved flight performance could be used to increase the feeding ability of the parents. This would result in the ability to raise more young, to raise the young faster, or to bring the young into "better" condition (i.e., the young should have a higher probability of survival and thus, future reproduction; Freed 1981; Norberg 1981; Jones 1987d). In addition, the increased maneuverability and faster take-offs associated with lower body mass would make a bird less susceptible to predation (Blem 1975; Nolan and Ketterson 1983; Lima 1986; Slagsvold and Lifjeld 1990). Mass loss should occur even when food is abundant, presumably through changes in the intensity or the amount of time devoted to feeding (Gaston and Jones 1989). Thus, the loss of mass by parents feeding young may be an adaptation to the energetic demands imposed by the young rather than a consequence of those demands. If this is the case, then it might be expected that mass loss would occur prior to maximum energy demand of the brood preparing adults for the increased flight time necessary to make the foraging trips for the rapidly growing young.

Although mass loss is likely to involve costs because it may leave the parents more susceptible to poor foraging conditions (Bryant and Westerterp 1983; Lima 1986; Jones 1987b; Blem 1990; Ekman and Hake 1990), the potential benefits in terms of higher fitness may outweigh these costs and make it advantageous for a bird to lose mass (Norberg 1981). Theoretically, adult birds should have an optimal mass, preprogrammed through adaptation, below which their survival declines (Nur 1984a,b; Crick and Fry 1986; Jones 1987d). Since many passerines breed when conditions are most favourable, a loss in fat reserves during this time would not be as costly as it would be if the loss occurred during less favourable conditions (Bryant and Westerterp 1983). Many birds increase their energy reserves when conditions are less favourable and foraging success is unpredictable (e.g., to ensure survival through the winter; Ekman and Hake 1990; Hurly 1992). These extra energy reserves would serve as a buffer against extreme conditions,

allowing birds to survive periods when energy intake is low. Presumably, the adjustment of energy reserves occurs with regard to energy requirements and environment predictability (McNamara and Houston 1990; Hurly 1992). The cost of carrying extra reserves must be balanced against the benefits gained by using the extra reserves as an insurance buffer against starvation (Ekman and Hake 1990). Thus, the costs and benefits of body mass loss change depending on specific circumstances such as climatic conditions and/or interactions with conspecifics and heterospecifics in the community.

Although mass loss appears to have important implications for the breeding biology of many birds, testing the various hypotheses used to explain its patterns has not received much attention. While several studies have indicated that the loss of body mass during the nestling period is evidence of reproductive stress, only Norberg (1981) and Freed (1981) have formally proposed that mass loss is an adaptation to reduce power consumption in flight during feeding trips. A major problem is that few studies have followed the body mass variations of specific individuals throughout the breeding season (Moreno 1989a; but see Carpenter et al. 1983; Crick and Fry 1986; Jones 1987a-d; Moreno 1989b). Since capturing birds by hand may cause stress, and even mass loss (Clark 1979; Brunet and Cyr 1990), most researchers capture individuals of their study population only once during the breeding season, usually at the time of banding. For this reason, most researchers have only a general picture of the patterns of variation in body mass for a particular population. Without following the body mass changes of undisturbed individuals, it is difficult to determine the timing and degree of body mass variation. Without a clear indication of when the changes occur and their extent, it is difficult to determine why mass variation exists and what significance it has to avian breeding biology and life history strategies. For example, if mass loss occurs early in the incubation stage, it might be evidence of gonadal atrophy. If mass loss occurs late in incubation or early in the nestling period, it may reflect a power saving advantage related

to flight, and if it occurs late in the nestling period when the demands of the young are greatest, it might reflect the stress of caring for the young.

The purpose of this study, therefore, was to investigate in detail the body mass variation of a passerine species during the breeding season, with particular emphasis on the body mass loss during the nestling period. I first documented the patterns of mass variation and then tested the relevant hypotheses concerning body mass variation using a food supplementation experiment. Although the two major hypotheses are not entirely mutually exclusive (see Gaston and Jones 1989), because mass loss induced by stress may result in savings in energy expended in flight because of decreased wing loading, the two hypotheses yield different predictions about the timing of mass loss. Below, I make predictions for body mass changes in adults rearing young according to the stress and flight adaptation hypotheses. Predictions are made concerning the timing of mass loss within the nesting cycle, mass loss patterns in the second brood attempt, year to year variation, and body mass changes during the food supplementation experiment.

a) According to Norberg's (1981) flight adaptation hypothesis, body mass loss should occur before the period of greatest energetic demand on the parents (i.e., before the mid or late nestling period) since the benefits of mass loss would prepare the parents for that demand. In other words, body mass loss by the adults should follow a decelerating or concave pattern once the nestlings hatch (Fig. 1). Mass loss seen as the nestlings grow, with the greatest loss at the time of maximum nestling demand would be evidence in support of the stress of reproduction hypothesis. Thus, mass loss in adults should accelerate as the nestlings grow, following a convex pattern (Fig. 1). Mass loss immediately after laying would be evidence for gonadal atrophy, especially in females.

b) According to the flight adaptation hypothesis, if there is a benefit to increased mass for laying and incubation, females attempting a second brood should regain mass prior to egg laying and then lose mass in a pattern and at a rate similar to that in the first brood attempt. Males attempting a second brood should not regain the mass as they need

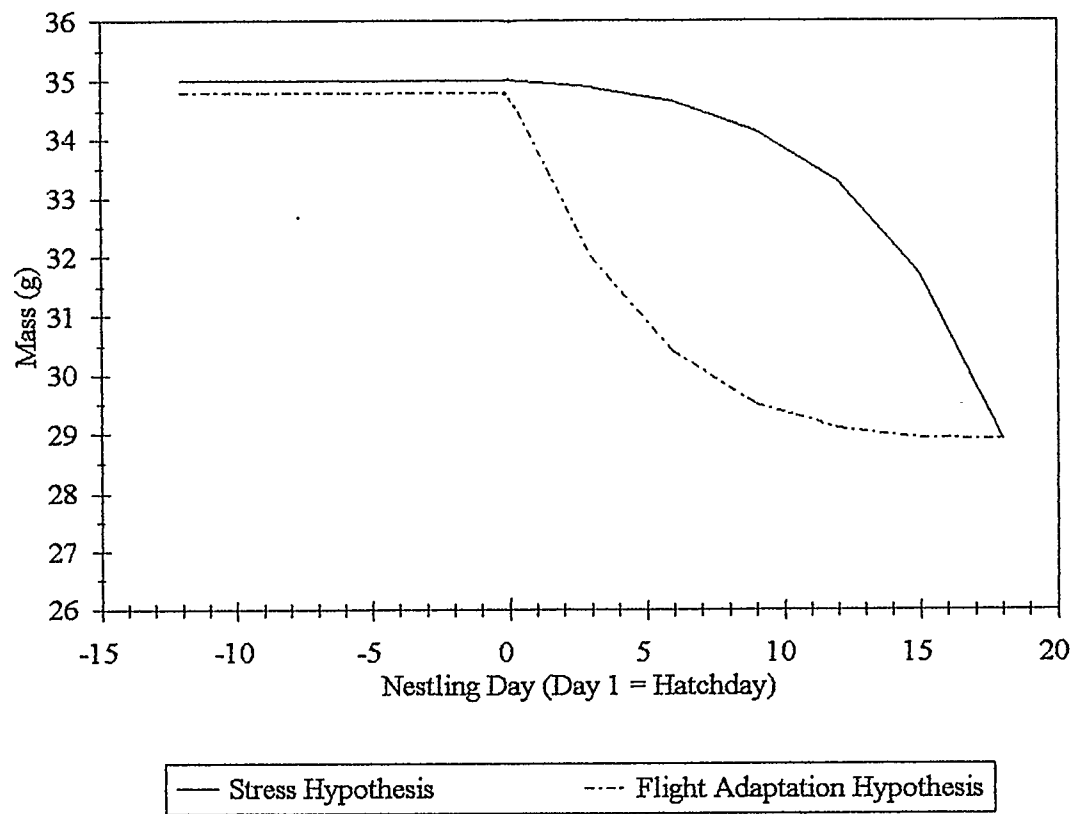


Fig. 1. Predictions for the patterns of body mass loss for adult females rearing young according to the stress and flight adaptation hypotheses.

to remain as light as possible to care for the young from both breeding attempts.

According to the stress hypothesis, both sexes would regain mass for the second brood and would not lose mass unless stress again became a factor.

c) According to the flight adaptation hypothesis, minimum body mass should be the same from year to year, as there is an optimal body mass for flight at each stage of the nesting cycle. Thus, in two different years, similar patterns of mass loss should be seen each year regardless of the conditions. According to the stress hypothesis, parents should lose more mass or lose mass at a faster rate in a colder, wetter year when food is scarce or difficult to obtain.

d) In good conditions, such as those created by food supplementation, the flight adaptation hypothesis predicts that supplemented birds should lose mass in a pattern and at a rate similar to that of control birds because there is an optimal body mass for flight. According to the stress hypothesis, supplemented birds should not lose mass or should lose less mass than control birds because some of the stress of reproduction has been removed.

To test these predictions, I used a sexually dimorphic, insectivorous passerine, the Mountain Bluebird (*Sialia currucoides* Bechstein), as my study species. I obtained accurate body mass variation patterns for undisturbed individuals during the first and second breeding attempts in two different years. I also obtained sex specific flight time budgets to determine the amount of time spent in flight during the different stages of the breeding season. In addition, I examined the growth patterns of the nestlings in control nests in both years. Finally, I performed a food supplementation experiment in which I supplemented 20 pairs and their young with 25 % of their daily energy needs. Food supplementation began on the second day of incubation and continued uninterrupted until the nestlings fledged. I then compared the body mass variation patterns between control and supplemented adults in the experiment and the nestling growth patterns between control and supplemented nests.



## METHODS AND MATERIALS

### The Study Species

The Mountain Bluebird is a member of the thrush family, Turdidae. Individuals are sexually dimorphic in plumage. The male has sky blue upper parts, including the wings and tail, and paler blue under parts with white on the abdomen. The female is brownish gray above, with pale blue in her wings, rump, and tail. Adults can be sexed based on the plumage difference (Zeleny 1976; Shantz 1986). In addition, nestling sex can be determined by the brightness of the primary wing feathers once the young reach Nestling Day 14 (Shantz 1986; Scriven 1990).

Mountain Bluebirds breed from Alaska in the North to Texas in the South, and from British Columbia in the West across to Manitoba in the East. They winter in Mexico, the Southwestern United States, and Southwestern British Columbia (Shantz 1986).

Mountain Bluebirds are insectivorous, secondary cavity nesters that take readily to man-made nest boxes (Power 1980). They are opportunistic foragers, eating primarily insects and spiders, including Coleoptera, Diptera, Ephemeroptera, Lepidoptera adults and caterpillars, Orthoptera, earthworms, and various larvae (Cummings 1986; Shantz 1986). Food items fed to young less than six days old are small and soft bodied (Shantz 1986). Weather, time of day, and season affect the diet. Mountain Bluebirds are perch and sally foragers, which means that foraging takes place from an elevated perch (Zeleny 1976; Shantz 1986; Scriven 1990). When a prey item is located, the Mountain Bluebird flies to the ground to capture it. When perches are not available or during inclement weather, the birds may forage on the ground or hover overhead (Shantz 1986; personal observation).

Mountain Bluebirds return to the breeding areas in central Alberta in late February or early March. Males establish territories around existing nest boxes and

attract females. Usually only the female builds a grass cup nest. The entire nesting cycle takes about seven weeks. Mountain Bluebirds lay their eggs in the beginning of May, and clutch size ranges from four to seven eggs, with smaller clutches laid later in the season. Incubation begins on the day the last egg is laid (Incubation Day 1, hereafter referred to as Inc 1), and all the eggs usually hatch on the same day (Nestling Day 1, hereafter referred to as ND 1). Only the females have brood patches, and they alone incubate the eggs and brood the young. The female will leave the eggs at regular intervals to forage for herself, and the male will occasionally feed the female during this time. The incubation period lasts approximately 14 days, with hatching occurring from mid-May to early July. Because the young are altricial, the female must brood for the first six days until they can thermoregulate, and both parents must provide the nestlings with food. The nestling period lasts approximately 21 days. The fledgling period may last two weeks or more, with the male looking after the fledglings if the pair attempts a second nest. Only about 25 % of the pairs in central Alberta attempt a second nest (M. Pearman, personal communication).

Mountain Bluebird predators include feral and domestic cats (Felis catus), American Crows (Corvus brachyrhynchos), Black-billed Magpies, snakes, weasels (Mustela spp.), and raccoons (Procyon lotor).

### **The Study Area**

I conducted field work at the Ellis Bird Farm Ltd., near Lacombe, Alberta, Canada (52° 28' N, 113° 43' W) between April and August 1991 and 1992. Lacombe (elevation 847 m ASL) typically has cold winters and short, warm summers. The mean annual temperature is 8.4 °C (Environment Canada 1982). The maximum and minimum recorded temperatures were 38.3 °C and -49.4 °C, respectively (Environment Canada

1982). The mean annual precipitation is 326.3 mm, and mean annual snowfall is 122.7 cm (Environment Canada 1982).

The study area is primarily crop land and pasture, including crops of winter wheat, spring wheat, canola, barley, and alfalfa. There were over 600 nest boxes available on the 100 km<sup>2</sup> study area, and approximately 100 pairs of Mountain Bluebirds nested each year. Nest boxes were set up in tandem, approximately 10 m apart, to reduce competition between Mountain Bluebirds and Tree Swallows (Tachycineta bicolor). Other competitors for the nest boxes included wasps, bumblebees, deer mice (Peromyscus maniculatus), House Wrens, Black-capped Chickadees (Parus atricapillus), woodpeckers (Picoides spp.), House Sparrows (Passer domesticus) and European Starlings. Nest boxes were located along roadsides on fence posts, approximately 1.0 to 1.5 m above the ground, and were monitored regularly to determine where Mountain Bluebirds were nesting, clutch initiation date, clutch size, hatch date, brood size, and fledge date. The Ellis Bird Farm attempted to box-trap and colour-band every adult in the population each year. In addition, once nestlings reached adult mass, they were colour banded by either me or the Ellis Bird Farm personnel. All individuals used in the study were successfully colour banded to facilitate individual identification.

### **The Weighing Apparatus and the Weighing Procedure**

I used two portable electronic balances (Sartorius PT600) with a capacity of 610 g and a precision of 0.1 g to obtain masses. I constructed a 20 cm "T" shaped dowel-rod perch and inserted it into a wooden block attached to the weighing pan of the balance. I placed the balance inside a padded wooden box to protect it from wind, rain, and bird droppings (Fig. 2). A small hole in the back of the box allowed a cable from the RS 232 output to interface with a digital display (Sartorius 737101A) or a portable computer. Although the portable computer allowed immediate data storage and took readings when conditions were unstable (i.e., high winds and moving birds), it was only used for a few

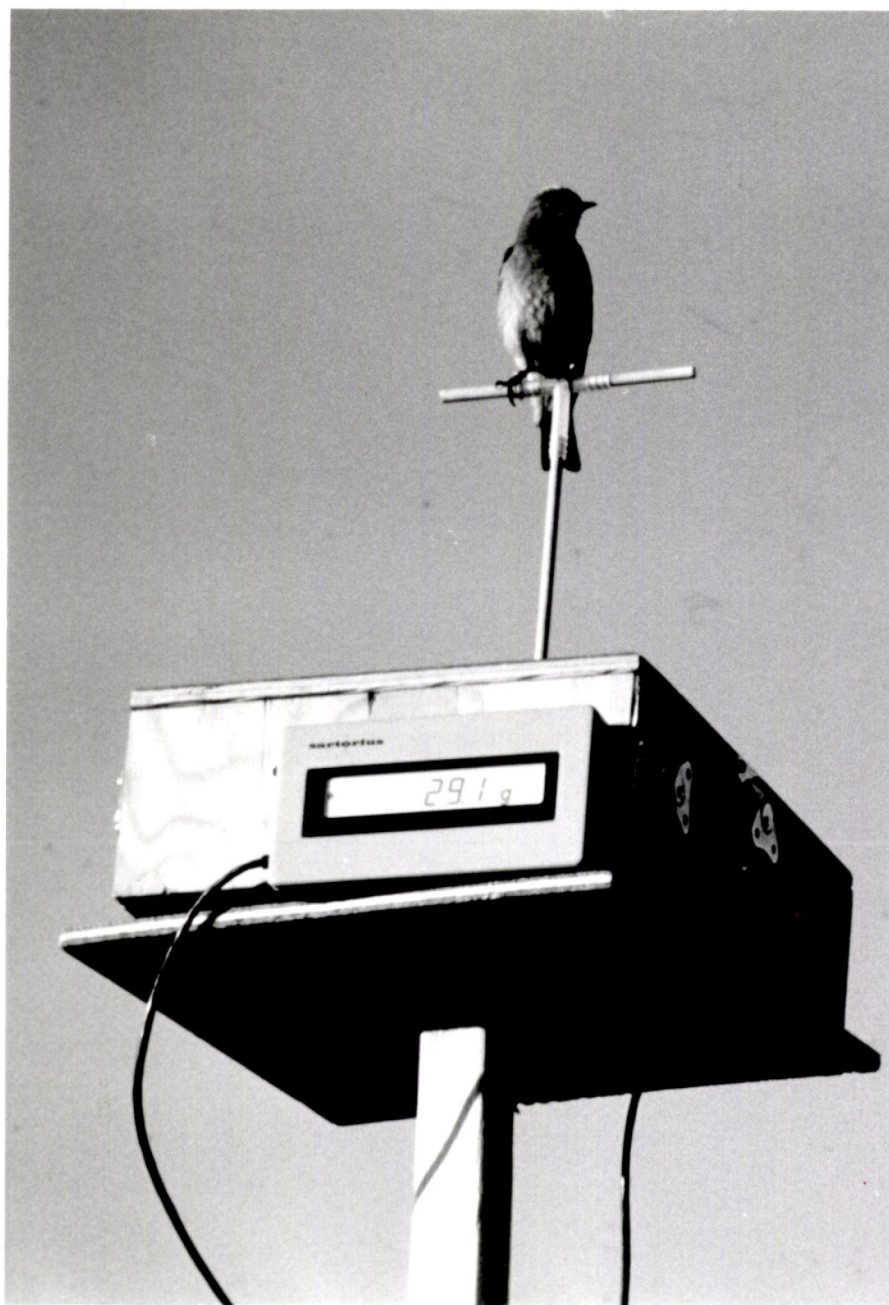


Fig. 2. Female Mountain Bluebird on the weighing apparatus.

weeks in May of 1991. Data collection proved to be much faster and more efficient using the digital display. When the birds landed on the perch, I used a vehicle as a blind and read the digital display from distances of up to 200 m using binoculars or a spotting scope.

To obtain adult masses, I placed the weighing apparatus in front of a nest box on a tripod, a fence post, or a wooden stake. The wooden stake was part of a "dummy perch" left continuously in front of each occupied nest box in the study area to habituate birds to the weighing apparatus. Dummy perches consisted of a 5 x 5 cm stake, a 30 x 30 cm wood platform, and a 20 cm tall "T" shaped dowel-rod perch. I erected dummy perches in each territory at the first sign of Mountain Bluebird activity (i.e., nest building). Placement of the dummy perches in each territory varied depending on differences in local topography and the behaviour of individual birds. In most cases, the dummy perch was located about 1 m from the nest box, directly in front of the nest hole. With this set-up, most birds landed on the perch when entering or exiting the box. Virtually all adults habituated to the dummy perch within an hour of its placement at the nest box, and when the weighing apparatus was present, birds landed on the perch within a few minutes and some within seconds.

In 1992, I taped a food reward (a mealworm larva, Tenebrio molitor) on the perch to attract the birds more rapidly. This also attracted birds that were reluctant to land on the perch, and ensured that the birds would remain on the perch long enough to obtain a stable reading of mass. The mealworms did not significantly affect adult mass as the mealworms weighed only 0.1 g, and the balance was tared once the mealworms were in place.

In 1991, a few females were caught on the nest during incubation or brooding. They were then weighed using a Pesola spring scale, accurate to 0.1 g. To decrease disturbance at the nest and to reduce nest desertion, I discontinued this method of obtaining masses after a few attempts. In 1992, birds were handled only at the time of

banding by personnel of the Ellis Bird Farm.

## **Observations**

### **Mass Data**

I collected mass data on 23 pairs of Mountain Bluebirds in 1991 and 47 pairs in 1992. I used only pairs with clutches of five or six eggs. Masses were obtained between sunrise and 12:00 noon each morning. I attempted to obtain these data from the prelaying stage through to fledging. Unfortunately, the birds were fairly secretive during prelaying and laying, and therefore, most of the mass data came from the incubation and nestling stages. The pairs and their young were virtually impossible to follow during the fledgling period, and masses were not taken during this stage. In 1991, I collected data every second day during incubation, beginning with Inc 2 and continuing until hatching. After hatching and beginning with ND 2, I again collected data every second day until the nestlings fledged. In 1992, this pattern was continued with both control and experimental nests (see below). In addition, to document mass changes around the time of hatching, I obtained mass data every day on control pairs from Inc 12 through ND 4.

During the nestling period, adults feeding nestlings occasionally landed on the perch with a food item(s) in their beaks. When this occurred, I attempted to obtain an adult mass after the adult had re-emerged from the nest box having fed its young.

### **Time Budget Data**

In 1991, I collected time budget information for 13 pairs of Mountain Bluebirds. Activities included time-in-flight, time sitting, and for females, time incubating the eggs and brooding the young. I collected data in the early evenings, from 18:00 until dusk in half-hour observation periods. For each pair, I collected these data five times during the breeding cycle: twice during incubation (Inc 5 or 6 and Inc 10 or 11), and three times during the nestling period (ND 3 or 4, ND 10 or 11, and ND 17 or 18). This represented

early and late incubation and the early, middle, and late nestling periods. I allowed two days for each data collection period to allow me to avoid inclement weather. In 1992, I collected data on the same daily activities for 10 pairs of Mountain Bluebirds. Again, I collected data from 18:00 until dusk, and the same activities were noted with the addition of feeding rate during the nestling period (number of feeding trips per young per hour). However, I collected data in one-hour observation periods and also collected data in the mornings from dawn to approximately 09:00. In 1992, data were collected seven times during the breeding cycle: Inc 5 or 6, Inc 10 or 11, Inc 13, ND 1, ND 3 or 4, ND 10 or 11, and ND 17 or 18.

#### **Nestling Data**

In 1991, I collected data on nestling growth for each nestling in all 23 nests. Data consisted of mass measurements (taken to the nearest 0.1 g using the electronic balance) and tarsus measurements (to the nearest mm using calipers). These measurements were taken on ND 3, 6, 9, 12, 15, and 18. In 1992, I collected the same data on nestlings in all control and experimental nests (see below). However, data were only collected on ND 6, 12, and 18. For identification purposes, I individually marked all nestlings with nail polish until they were large enough to be permanently marked on ND 12 with colour bands and a Fish and Wildlife Service band.

#### **The Food Supplementation Experiment**

In 1992, I performed a food supplementation experiment to address the relevant hypotheses concerning mass variation. In this experiment, I gave 20 pairs of Mountain Bluebirds an estimated 25 % of their daily energy needs while 27 control pairs were not given additional food. Only birds with clutches of five or six eggs were used. I then compared adult mass changes, reproductive success, and nestling growth between the two groups. On Inc 2, I assigned nests randomly to either control or supplemental food

groups. Control pairs did not receive supplemental food but were monitored at the same rate as supplemented pairs. Supplementation consisted of mealworm larvae provided in small aluminum baking tins at the nest box. Supplementation began on the second day of incubation so that laying date, clutch size, and egg size would not be affected (see Arcese and Smith 1988 and references therein; Nilsson 1991). Supplementation continued until the nestlings fledged from the nest. If the pair attempted a second brood, the period between broods was not supplemented so that laying date, clutch size, and egg size of the second attempt were once again not affected. Supplementation for the second attempt then began on Inc 2.

I gave food supplements once a day, between dawn and 10:00. Virtually all supplemented pairs found the food within minutes of its placement at the nest box. All pairs used in the study had found, and were consuming, mealworms from the containers by Inc 3, the second day of food placement in the territory. Observations were made to insure that all mealworms were consumed only by the members of each pair and their young. Mass data and nestling growth data were collected for both treatments following the procedures outlined above. Time did not allow me to obtain time activity budget data on supplemented pairs.

Western Bluebirds (*Sialia mexicana*), a closely related and similar sized species, require 95 kJ of energy per day per adult when feeding nestlings (Mock 1991). Because Mountain Bluebirds weigh slightly more than Western Bluebirds, I estimated that Mountain Bluebirds would require approximately 100 kJ of energy per day per adult. Fifty kJ would then represent supplementing 25 % of the daily energy needs for a pair. In general, birds metabolize the energy available in an average insect with a minimum efficiency of 71.2 % (Bell 1990). Live mealworms have a higher lipid content than most insects but are similar in water and energy content with 11.59 kJ per g (Bell 1990). Thus, mealworms would provide 8.25 kJ per g. This means that during incubation, a pair of Mountain Bluebirds must be given 6.1 g of mealworms (approximately 55 mealworms)



per day to supplement their daily energy needs by 25 %. Similar calculations were made for the nestling period, taking into account the number of nestlings and the changing energy demands as the nestlings grow (see Mock 1991). For example, on ND 6, a Western Bluebird nestling requires 46 kJ per day (Mock 1991). For a brood of five young, the requirements would increase to 230 kJ plus the 200 kJ required by the parents. Thus, 107.5 kJ would represent supplementing a pair and their five young by 25 %. This would amount to 13.0 g of mealworms or 119 mealworms total. On ND 12, a Western Bluebird nestling requires 65 kJ (Mock 1991). Using the same calculations, a pair and their five young must be supplemented with 15.9 g of mealworms.

### Statistical Analysis

Unless otherwise stated, all values are reported as mean  $\pm$  standard error. I analyzed the adult Mountain Bluebird mass data using SAS statistical software (SAS Institute Inc. 1985). The effects of weather, time of day, reproductive stage, clutch size, brood size, and age on mass were analyzed using Analysis of Covariance (ANCOVA). In addition, differences in patterns of mass variation between the sexes, between brood attempts, between years, and between treatments in the food supplementation experiment were also analyzed using ANCOVA. Mass was the dependent variable, day in the breeding cycle was the covariate, and individual bird was a random variable in the ANCOVA models. Within the ANCOVA models, all slopes involving the rate of mass change were compared to a slope of zero to determine if the mass change was significant. When three-way interactions were significant, slopes were compared using the Bonferroni correction factor. The corrected significance level was  $0.0127 (\alpha_c = 1 - (1 - \alpha)^{1/s}; \text{ where } s \text{ in this case was four})$ .

To test the prediction regarding the shape of the mass loss curves, female mass data from hatching were analyzed using a regression model (SAS Institute Inc. 1985) incorporating day in the breeding cycle (DAY and DAY\*DAY), with individual bird as a

random variable. A significant negative effect of DAY\*DAY would indicate decelerating mass loss consistent with the flight adaptation hypothesis, while a significant positive effect of DAY\*DAY would indicate accelerating mass loss consistent with the stress hypothesis. The shape of the mass loss curves were compared between years for control females and between experimental and control females for 1992.

Data were also analyzed using Statistix (1987) analytical programs. Student's t tests and chi-squared tests of two by two contingency tables were used for other comparisons involving weather data, nestling growth data, adult time budget data, and life history traits (i.e., egg 1 date, clutch size, hatch date, and brood size) unless otherwise stated. On the few occasions when means had unequal variances, the Welch's approximate t was used (Zar 1984). Statistical tests employed a significance level of 0.05 unless otherwise stated.

## RESULTS

### OBSERVATIONS

#### The Study Site

In 1991, the first Mountain Bluebirds returned to the study area on March 16. There were 599 nest boxes available. Approximately 120 pairs of Mountain Bluebirds attempted first nests, and 42 pairs attempted second nests. The first egg was laid on April 25. In total, 850 eggs were laid, 669 eggs hatched (79 %), and 605 young fledged (71 % of the eggs laid). It was the most productive year in the history of the Ellis Bird Farm (Pearman 1991). I used 23 pairs for my observations, and eight of these pairs attempted second nests.

In 1992, Mountain Bluebirds returned to the study area on March 10. There was a decrease in the number of nest boxes available, down to 504, because of construction

on the Union Carbide Plant and road construction by the County of Lacombe.

Approximately 116 pairs attempted first nests, and 15 pairs attempted second nests. The first egg was laid on April 27. In total, 755 eggs were laid, 477 eggs hatched (63 %), and only 389 young fledged (52 % of the eggs laid). It was one of the least productive years in the Ellis Bird Farm history (Pearman 1992). I used 47 pairs for my observations and the supplementation experiment. Of the 47 pairs, 12 attempted second nests. In both years, but especially in 1992, nests were preyed upon by either Black-billed Magpies or weasels. Nests were also lost to House Wrens and House Sparrows, both fierce competitors for the nest boxes.

## Weather

Fluctuations in mean daily temperature for both the 1991 and the 1992 breeding seasons are shown in Figure 3. The number of days in May 1991 which were warmer than the same day in 1992 was not different from that expected by random chance ( $X^2 = 0.32$ , d.f. = 1,  $p > 0.50$ ). The number of days in June 1992 which were warmer than the same day in June 1991 was significantly more than expected by random chance ( $X^2 = 6.54$ , d.f. = 1,  $p < 0.02$ ). The number of days in July 1991 which were warmer than the same day in 1992 was significantly more than that expected by random chance ( $X^2 = 3.90$ , d.f. = 1,  $p < 0.05$ ). Mean minimum, daily, and maximum temperatures for each month during the study are shown in Table 2. May temperatures were not different between years (min,  $t = 1.22$ , d.f. = 62,  $p > 0.20$ ; mean,  $t = 1.10$ , d.f. = 62,  $p > 0.25$ ; max,  $t = 0.76$ , d.f. = 54.9,  $p > 0.45$ ). While there was no difference in June minimum temperatures, the daily mean and maximum temperatures were greater in 1992 (min,  $t = 1.31$ , d.f. = 60,  $p > 0.15$ ; mean,  $t = 2.38$ , d.f. = 49.9,  $p < 0.05$ ; max,  $t = 2.50$ , d.f. = 49.6,  $p < 0.02$ ). All July temperatures were greater in 1991 (min,  $t = 2.06$ , d.f. = 56.8,  $p < 0.05$ ; mean,  $t = 3.21$ , d.f. = 62,  $p < 0.005$ ; max,  $t = 2.67$ , d.f. = 62,  $p < 0.01$ ). Thus, May temperatures were cooler in 1992, although not significantly so. June was warmer in

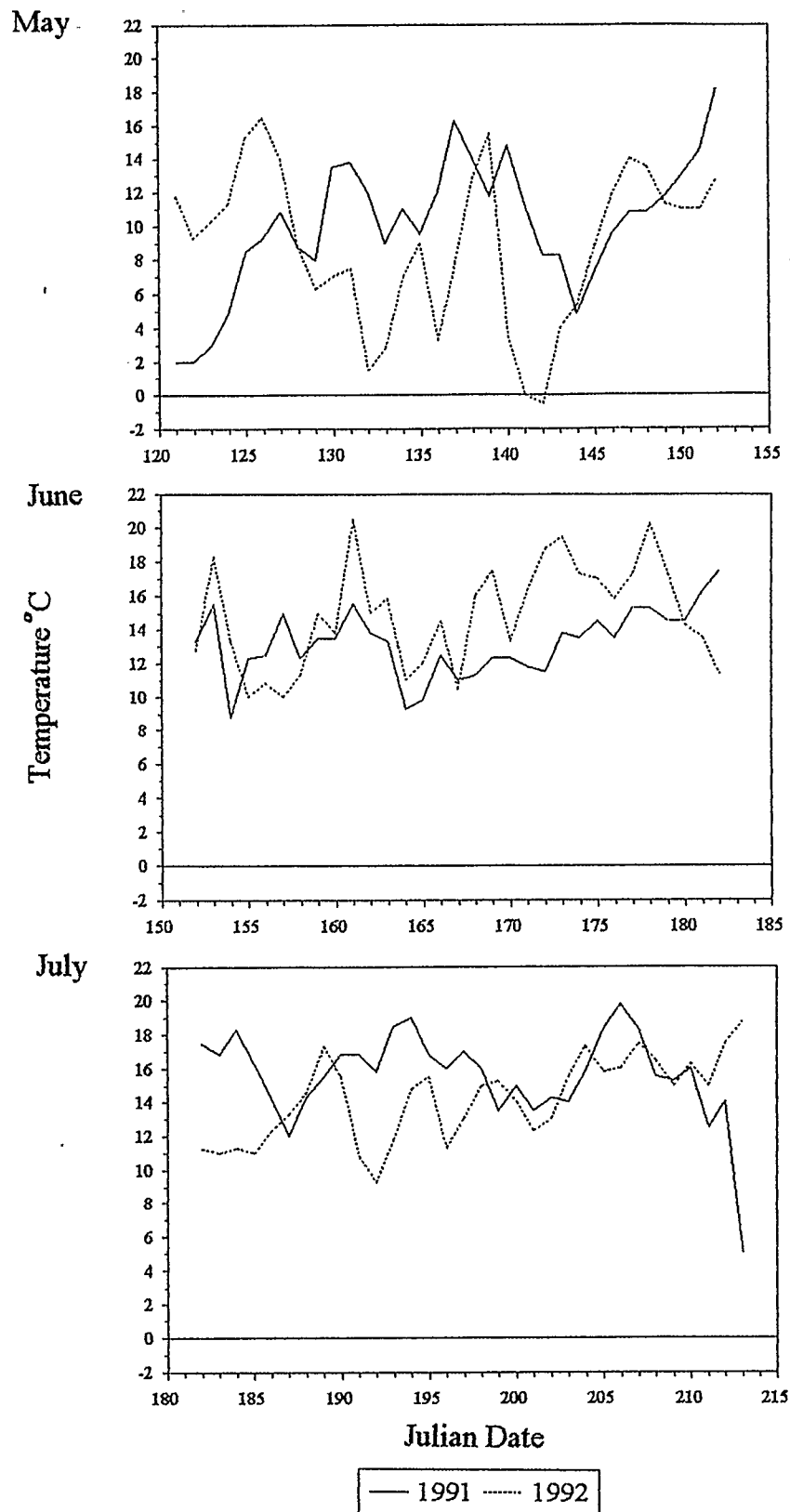


Fig. 3. Fluctuations in mean daily temperature in degrees Celsius by Julian date for the months of May, June, and July in both the 1991 and the 1992 breeding seasons.

Table 2. Mean ( $\pm$  SE) minimum, daily, and maximum temperatures in degrees Celsius and number of days with rain in mm for each month during the breeding season in 1991 and 1992. Temperatures that are significantly different between years are marked with an asterisk.

|                                   | MAY            |                | JUNE           |                  | JULY           |      |                |
|-----------------------------------|----------------|----------------|----------------|------------------|----------------|------|----------------|
|                                   | 1991           | 1992           | 1991           | 1992             | 1991           | 1992 |                |
| Mean Daily Minimum Temperature    | $3.5 \pm 0.7$  | $2.3 \pm 0.6$  | $7.8 \pm 0.4$  | $8.7 \pm 0.5$    | $9.2 \pm 0.4$  | *    | $7.8 \pm 0.6$  |
| Mean Daily Temperature            | $10.0 \pm 0.7$ | $8.9 \pm 0.8$  | $13.2 \pm 0.3$ | * $14.7 \pm 0.6$ | $15.9 \pm 0.3$ | *    | $14.2 \pm 0.4$ |
| Mean Daily Maximum Temperature    | $16.6 \pm 0.9$ | $15.4 \pm 1.3$ | $18.5 \pm 0.5$ | * $20.9 \pm 0.8$ | $22.6 \pm 0.5$ | *    | $20.6 \pm 0.6$ |
| Number of Days with Rain (> 1 mm) | 7              | 11             | 17             | 8                | 14             |      | 10             |

1992, and July was warmer in 1991. Number of days with rain greater than one mm is also shown in Table 2. There were more days with rain in May of 1992 than in May of 1991, however this difference was not significant ( $X^2 = 0.70$ , d.f. = 1,  $p > 0.40$ ). June and July of 1991 had more days with rain than did June and July in 1992. This difference was only significant in June (June,  $X^2 = 4.39$ , d.f. = 1,  $p < 0.05$ ; July,  $X^2 = 0.06$ , d.f. = 1,  $p > 0.75$ ).

There were major storms in mid-May each year. The storm in 1992 was much worse than the storm in 1991, with a combination of snow and sub-freezing temperatures. Most of the Mountain Bluebirds were still incubating eggs at this time, and females appeared to abandon temporarily their clutches, only returning once the weather improved. Incubation periods were extended by several days. A few nests had small young at the time of the storm. Parents in two of the three control nests that had young, abandoned their nests. The young subsequently died of starvation and/or hypothermia. Three supplemented pairs with young did not desert their nests. However, the nestlings from these nests had slower growth than nestlings hatched after the storm (ND 6 mass,  $t = 7.05$ , d.f. = 90,  $p < 0.001$ ; tarsus,  $t = 5.01$ , d.f. = 90,  $p < 0.001$ ; ND 12 mass,  $t = 4.95$ , d.f. = 81,  $p < 0.001$ , tarsus,  $t = 4.04$ , d.f. = 81,  $p < 0.001$ ; ND 18 mass,  $t = 1.99$ , d.f. = 75,  $p < 0.05$ , tarsus,  $t = 0.98$ , d.f. = 75,  $p > 0.30$ ). Thus, the early snowstorm in May of 1992 had an effect on incubation behaviour of the females, hatching success, and nestling growth and survival.

## **Adult Behaviour**

### **Time Activity Budgets**

For both years, time activity patterns in the early evenings are shown in Table 3. In 1991, males consistently flew more than females did, and both sexes flew the most during the early nestling stage. However, the pattern of variation in flight time over the

Table 3. Proportion of time spent flying, sitting, and incubating by females and males in both years and both observation periods. Sample size ranged from 9 to 11 individuals. Significant differences between years are marked with an asterisk (\*), and significant differences between morning and evening in 1992 are marked with a bullet (•). Data were not collected on Inc 13 and ND 1 in 1991, females do not brood after ND 6, and males do not incubate or brood at all.

| FEMALES: | Time Spent Flying |        |        | Time Spent Sitting |        |        | Time Spent Incubating or Brooding |        |        |
|----------|-------------------|--------|--------|--------------------|--------|--------|-----------------------------------|--------|--------|
|          | 1991              | 1992   |        | 1991               | 1992   |        | 1991                              | 1992   |        |
|          | p.m.              | p.m.   | a.m.   | p.m.               | p.m.   | a.m.   | p.m.                              | p.m.   | a.m.   |
| Inc 5    | 0.04              | 0.04   | 0.04   | 0.31               | 0.28   | 0.34   | 0.65                              | 0.68   | 0.62   |
| Inc 10   | 0.03              | 0.05   | 0.04   | 0.41               | *      | 0.24   | 0.56                              | 0.71   | 0.69   |
| Inc 13   | ---               | 0.05   | • 0.03 | ---                | 0.41   | • 0.22 | ---                               | 0.54   | • 0.75 |
| ND 1     | ---               | 0.07   | 0.05   | ---                | 0.38   | 0.28   | ---                               | 0.55   | • 0.67 |
| ND 3     | 0.07              | 0.08   | 0.05   | 0.80               | *      | 0.54   | 0.13                              | * 0.38 | • 0.58 |
| ND 10    | 0.07              | * 0.13 | 0.16   | 0.93               | *      | 0.86   | ---                               | ---    | ---    |
| ND 18    | 0.06              | * 0.16 | 0.14   | 0.94               | *      | 0.84   | ---                               | ---    | ---    |
|          |                   |        |        |                    |        |        |                                   |        |        |
| MALES:   | Time Spent Flying |        |        | Time Spent Sitting |        |        |                                   |        |        |
|          | 1991              | 1992   |        | 1991               | 1992   |        |                                   |        |        |
|          | p.m.              | p.m.   | a.m.   | p.m.               | p.m.   | a.m.   |                                   |        |        |
| Inc 5    | 0.06              | 0.07   | 0.06   | 0.94               | 0.93   | 0.94   |                                   |        |        |
| Inc 10   | 0.04              | * 0.07 | • 0.11 | 0.96               | * 0.93 | • 0.89 |                                   |        |        |
| Inc 13   | ---               | 0.07   | 0.07   | ---                | 0.93   | 0.93   |                                   |        |        |
| ND 1     | ---               | 0.10   | 0.09   | ---                | 0.90   | 0.91   |                                   |        |        |
| ND 3     | 0.11              | 0.11   | 0.12   | 0.89               | 0.89   | 0.88   |                                   |        |        |
| ND 10    | 0.09              | 0.13   | 0.14   | 0.91               | 0.87   | 0.86   |                                   |        |        |
| ND 18    | 0.07              | * 0.14 | 0.11   | 0.93               | * 0.86 | 0.89   |                                   |        |        |

different stages was the same in both sexes (sex,  $F = 7.50$ , d.f. = 1, 24.17,  $p < 0.02$ ; stage,  $F = 9.75$ , d.f. = 4, 94,  $p < 0.001$ ; sex\*stage,  $F = 0.40$ , d.f. = 4, 94,  $p > 0.80$ ). When time in flight for both sexes at each stage was compared, there was no difference in time flying by males versus females in any one stage ( $t \leq 1.89$ , d.f.  $\geq 22$ ,  $p > 0.07$  in every case). In 1992, there was no difference in the amount of time spent in flight by either sex at the various stages, and the pattern of variation in flight time over the different stages was the same. However, both sexes flew the most during the mid and late nestling period (sex,  $F = 3.01$ , d.f. = 1, 46.79,  $p > 0.08$ ; stage,  $F = 9.82$ , d.f. = 6, 99,  $p < 0.001$ , sex\*stage,  $F = 0.76$ , d.f. = 6, 99,  $p > 0.60$ ).

In 1992, additional observations were made in the early morning (see Table 3). At this time, males flew more than females did, especially when females were incubating or brooding. Females flew more than did males during the mid and late nestling stages. The amount of time spent in flight at each stage, and the pattern of variation in flight time over the different stages was also different (sex,  $F = 7.34$ , d.f. = 1, 44.52,  $p < 0.01$ ; stage,  $F = 9.23$ , d.f. = 6, 98,  $p < 0.001$ ; sex\*stage,  $F = 3.41$ , d.f. = 6, 98,  $p < 0.005$ ). When time in flight at each stage was compared between sexes, the sexes differed in the amount of time they spent in flight only during the mid and late incubation stages (Inc 10 and 13) and the early nestling period (ND 1 and 3; Inc 10,  $t = 3.46$ , d.f. = 20,  $p < 0.002$ ; Inc 13,  $t = 2.54$ , d.f. = 19,  $p < 0.02$ ; ND 1,  $t = 2.45$ , d.f. = 18,  $p < 0.05$ ; ND 3,  $t = 4.03$ , d.f. = 19,  $p < 0.001$ ; for the remaining stages,  $t \leq 1.20$ , d.f.  $\geq 16$ ;  $p > 0.20$ ). Thus, in the morning when females were incubating or brooding, males spent more time in flight than females did.

I compared the amount of time spent flying by each sex in the morning and in the evening during each stage. Females spent the same amount of time in flight in the morning and the early evening except during late incubation (Inc 13) when they flew more in the evening (Paired t-test,  $t = 2.28$ , d.f. = 10,  $p < 0.05$ ; all other stages,  $t \leq 2.25$ , d.f.  $\geq 9$ ,  $p > 0.05$ ). Females spent more time sitting in the evening only during the late



incubation and early nestling stages (Inc 13,  $t = 3.98$ , d.f. = 10,  $p < 0.002$ ; ND 3,  $t = 2.32$ , d.f. = 10,  $p < 0.05$ ; all other stages,  $t \leq 1.92$ , d.f.  $\geq 9$ ;  $p > 0.08$ ). Finally, at the end of incubation and in the early nestling stage females spent more time incubating or brooding in the morning than in the evening (Inc 13,  $t = 3.45$ , d.f. = 10,  $p < 0.01$ ; ND 1,  $t = 2.34$ , d.f. = 9,  $p < 0.05$ ; ND 3,  $t = 2.66$ , d.f. = 10,  $p < 0.05$ ; all other stages,  $t \leq 0.55$ , d.f.  $\geq 9$ ,  $p > 0.55$ ).

Males did not differ in the amount of time spent in flight in the morning versus the evening (Paired t-test,  $t \leq 1.38$ , d.f.  $\geq 9$ ,  $p > 0.20$ , in every case), except during mid incubation (Inc 10) when they flew more in the morning ( $t = 2.96$ , d.f. = 8,  $p < 0.02$ ). Males spent the same amount of time sitting in the morning and the early evening at every stage ( $t \leq 0.61$ , d.f.  $\geq 9$ ,  $p > 0.55$  in every case), except the mid incubation stage when they sat more in the evening ( $t = 2.96$ , d.f. = 8,  $p < 0.02$ ).

When only incubation and the early nestling stage were compared, females in both years spent more time incubating than brooding in the evening (Single factor ANOVA, 1991,  $F = 23.95$ , d.f. = 2, 36,  $p < 0.001$ ; 1992,  $F = 3.36$ , d.f. = 4, 49,  $p < 0.02$ ). Females in 1992 spent the same amount incubating or brooding in the morning ( $F = 0.87$ , d.f. = 4, 48,  $p > 0.45$ ). Females in 1992 spent the same amount of time incubating at each phase of incubation regardless of the time of day (a.m.,  $F = 0.86$ , d.f. = 2, 29,  $p > 0.40$ ; p.m.,  $F = 2.42$ , d.f. = 2, 29,  $p > 0.10$ ). In both the morning and evening, females spent the same amount of time brooding on ND 1 as they did on ND 3 (a.m.,  $F = 1.17$ , d.f. = 1, 19,  $p > 0.25$ ; p.m.,  $F = 1.92$ , d.f. = 1, 20,  $p > 0.15$ ). Thus, females spent the same time incubating regardless of date or time during incubation. This was also true for time spent brooding the young. However, overall females spent more time incubating eggs than they did brooding young.

### Feeding Rates

Feeding rates (number of feeding trips per young per hour) during both the 1992 morning and evening observation periods are shown in Table 4. On ND 1, both sexes fed the young at a greater rate in the morning than in the evening (Paired t-test, females,  $t = 2.30$ , d.f. = 9,  $p < 0.05$ ; males,  $t = 2.49$ , d.f. = 9,  $p < 0.05$ ). On ND 3, ND 10, and ND 18, both sexes fed at the same rate in the morning as they did in the evening (Paired t-tests,  $t \leq 1.54$ , d.f.  $\geq 8$ ,  $p > 0.15$ , in every case). Males fed more than females on the mornings of ND 1 and ND 3 when the females were brooding (Paired t-tests; ND 1,  $t = 2.54$ , d.f. = 9,  $p < 0.05$ ; ND 3,  $t = 2.46$ , d.f. = 9,  $p < 0.05$ ; all other observations,  $t \leq 1.60$ , d.f.  $\geq 8$ ,  $p > 0.10$ ).

### Nestling Growth Patterns

In both years, nestlings exhibited sigmoidal growth with rapid growth to asymptotic mass (approximately that of adults), followed by a leveling off until fledging (Fig. 4). The fastest growth occurred from ND 6 to ND 12 in both years. Tarsus development showed a similar trend, except the fastest growth occurred from ND 3 to ND 10 (Fig 5).

## PATTERNS OF ADULT BODY MASS VARIATION

### Time of Day

Each year mass data were collected between dawn and noon. The time of data collection was then placed into the 1991 ANCOVA models. There was no effect of time on female mass variation during either incubation or the nestling stage (Incubation: time,  $F = 2.40$ , d.f. = 1, 30,  $p > 0.10$ ; time\*day,  $F = 2.08$ , d.f. = 1, 30,  $p > 0.15$ ; Nestling stage: time,  $F = 1.73$ , d.f. = 1, 78,  $p > 0.15$ ; time\*day,  $F = 0.83$ , d.f. = 1, 78,  $p > 0.35$ ). Likewise, time did not affect male mass during incubation or the nestling period (Incubation: time,  $F = 0.20$ , d.f. = 1, 26,  $p > 0.65$ ; time\*day,  $F = 0.03$ , d.f. = 1, 26,  $p >$

Table 4. Mean ( $\pm$  SE) feeding rate in number of feeding trips per young per hour during various phases of the nestling period for both females and males in the morning and the evening in 1992. Significant differences between the sexes are denoted by an asterisk (\*), and significant differences between observation periods for both females and males are shown by a bullet (●).

|                 | Morning         |                   | Evening           |                 |
|-----------------|-----------------|-------------------|-------------------|-----------------|
|                 | Females         | Males             | Females           | Males           |
| ND 1<br>(Early) | $0.69 \pm 0.14$ | * $1.72 \pm 0.43$ | ● $0.49 \pm 0.15$ | $0.98 \pm 0.25$ |
| ND 3<br>(Early) | $0.77 \pm 0.20$ | * $1.24 \pm 0.18$ | $0.95 \pm 0.17$   | $1.07 \pm 0.20$ |
| ND 10<br>(Mid)  | $2.47 \pm 0.47$ | $1.86 \pm 0.34$   | $1.68 \pm 0.23$   | $1.52 \pm 0.29$ |
| ND 18<br>(Late) | $2.19 \pm 0.62$ | $1.54 \pm 0.41$   | $1.90 \pm 0.33$   | $1.77 \pm 0.27$ |

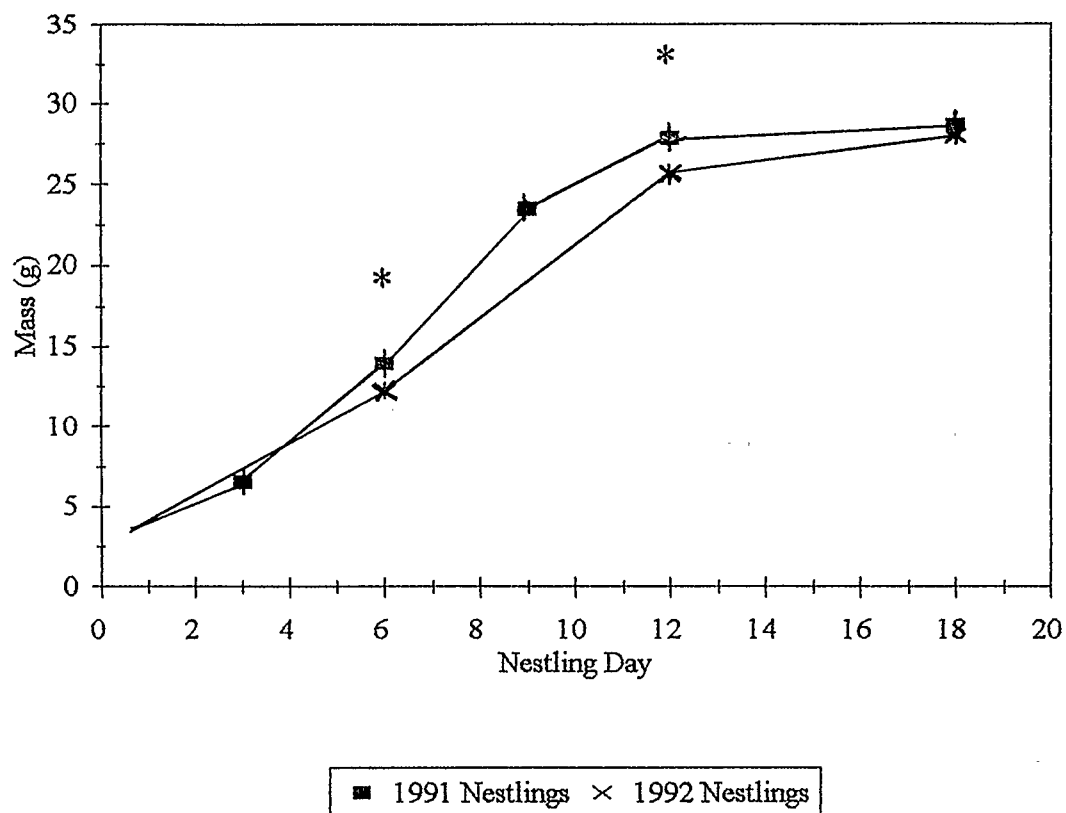


Fig. 4. Changes in mean nestling mass ( $\pm$  SE) during the 1991 and 1992 breeding seasons. Significant differences between years are marked by an asterisk (\*). Sample size varied between 104 and 121 nestlings.

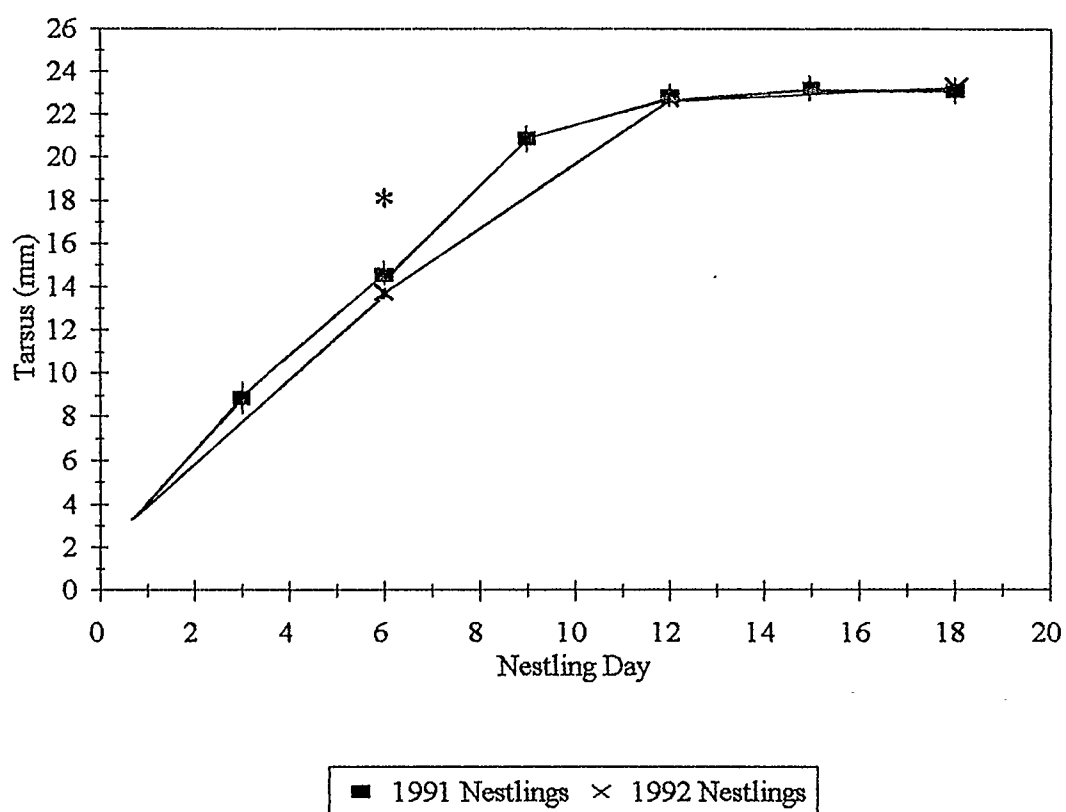


Fig. 5. Changes in mean nestling tarsus length ( $\pm$  SE) during the 1991 and 1992 breeding seasons. Significant differences between years are shown by an asterisk (\*). Sample size varied between 104 and 121 nestlings.

0.85; Nestling stage: time,  $F = 0.07$ , d.f. = 1, 68,  $p > 0.75$ ; time\*day,  $F = 0.07$ , d.f. = 1, 68,  $p > 0.75$ ). In addition, seven birds were weighed twice on the same day, several hours apart, and there was no difference between the two masses (Paired t-test,  $t = 1.02$ , d.f. = 6,  $p > 0.30$ ). Thus, time of day did not have an effect on mass.

## Weather

Using Lacombe weather data from Environment Canada, mean temperature on each day was included in the ANCOVA models. For females in 1991, temperature had no effect on mass or rate of mass change throughout the nesting cycle (temp,  $F = 0.07$ , d.f. = 1, 240,  $p > 0.75$ ; temp\*day,  $F = 2.15$ , d.f. = 1, 240,  $p > 0.10$ ). The same results were seen during both incubation and the nestling period (Incubation: temp,  $F = 0.39$ , d.f. = 1, 122,  $p > 0.50$ , temp\*day,  $F = 1.91$ , d.f. = 1, 122,  $p > 0.15$ ; Nestling stage: temp,  $F = 0.36$ , d.f. = 1, 110,  $p > 0.55$ ; temp\*day,  $F = 2.90$ , d.f. = 1, 110,  $p > 0.09$ ). Likewise, there was no effect of rain on female mass or the rate of mass change throughout the nesting cycle (rain,  $F = 0.16$ , d.f. = 1, 240,  $p > 0.65$ ; rain\*day,  $F = 0.44$ , d.f. = 1, 240,  $p > 0.50$ ). In addition, on Inc 12, female masses were plotted against temperature. Females at this stage in the nesting cycle did not have lower masses on colder days (Single factor ANOVA,  $F = 0.87$ , d.f. = 1, 17,  $p > 0.35$ ). This was also true when female mass on Inc 12 was plotted against temperature from the previous day ( $F = 0.75$ , d.f. = 1, 17,  $p > 0.35$ ). Thus, general variation in climatic conditions did not affect female body mass on a day to day basis or throughout the nesting cycle.

Weather variation also did not affect mass or rate of mass change in 1991 males during the nesting cycle (temp,  $F = 0.79$ , d.f. = 1, 232,  $p > 0.35$ ; temp\*day,  $F = 1.08$ , d.f. = 1, 232,  $p > 0.35$ ; rain,  $F = 2.10$ , d.f. = 1, 232,  $p > 0.10$ ; rain\*day,  $F = 0.78$ , d.f. = 1, 232,  $p > 0.75$ ). In addition, on Inc 12, males did not have lower masses at colder temperatures (Single factor ANOVA, same day,  $F = 0.18$ , d.f. = 1, 12,  $p > 0.65$ ). This was also true when mass on Inc 12 was plotted against temperature from the previous

day ( $F = 0.03$ , d.f. = 1, 12,  $p > 0.85$ ). Again, weather did not affect body mass, either on a daily basis or throughout the nesting cycle.

May 22 to May 24 were extremely cold, wet days in 1991. To determine if extreme weather had an effect on adult mass, I compared mass before the storm with masses during and immediately following the storm. There was no difference in male mass at any point during this period (Single factor ANOVA,  $F = 0.33$ , d.f. = 3, 16,  $p > 0.80$ ). Females, on the other hand, lost an average of 1.5 g during the storm and never regained that mass ( $F = 3.82$ , d.f. = 3, 24,  $p < 0.05$ ). In 1992, from May 19 to May 21, there was a snowstorm with subfreezing temperatures. Males lost an average of 1.0 g in two days, but returned to pre-storm mass immediately following the storm. The loss was not significant ( $t = 1.17$ , d.f. = 18,  $p > 0.25$ ). Females, however, lost an average of 2.5 g in two days (Paired t-test,  $t = 3.17$ , d.f. = 24,  $p < 0.005$ ), and never regained the lost mass. Thus extreme conditions had negligible effects on male mass and significant effects on female mass in both years.

### **Differences Between the Sexes**

Mass data were normally distributed, and thus, no transformations were necessary. In 1991, females began incubation much heavier than males, with a mean mass of  $35.2 \pm 0.6$  g ( $n = 8$ ) compared to a mean male mass of  $29.5 \pm 0.4$  g ( $n = 9$ ;  $t = 6.77$ , d.f. = 15,  $p < 0.001$ ). From the beginning of incubation through to the end of the nestling period, females lost an average of 0.15 g per day while males lost 0.03 g per day. These slopes were significantly different from zero (females,  $t = 15.17$ ,  $p < 0.001$ ; males,  $t = 3.31$ ,  $p < 0.005$ ; Fig 6). The sexes had different masses and lost mass at different rates (sex,  $F = 63.78$ , d.f. = 1, 45.55,  $p < 0.001$ ; sex\*day,  $F = 86.15$ , d.f. = 1, 474,  $p < 0.001$ ). At the end of the nestling stage, females had a mean mass of  $29.1 \pm 0.5$  g ( $n = 16$ ), and males weighed  $29.1 \pm 0.2$  g ( $n = 25$ ). There was no difference in body mass between the sexes at this time ( $t = 0.03$ , d.f. = 39,  $p > 0.95$ ).

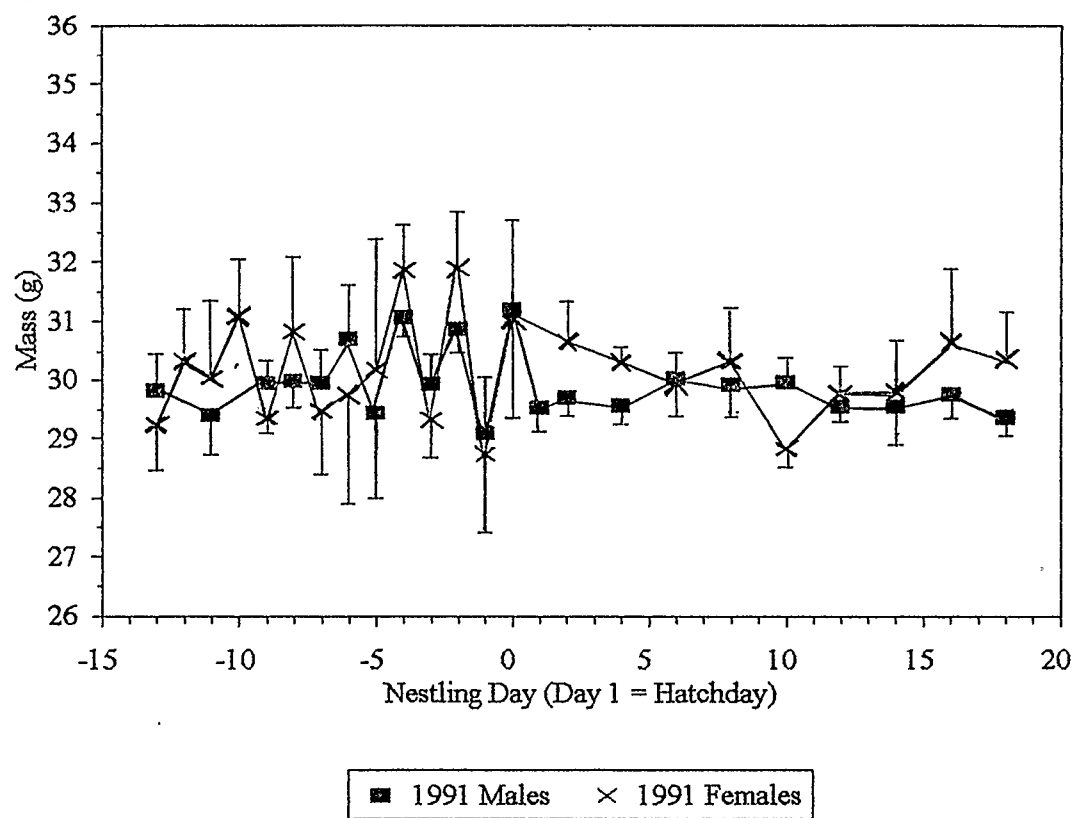


Fig. 6. Mass variation patterns in mean mass ( $\pm$  SE) by nestling day for males and females in 1991. Sample size ranged from 5 to 13 individuals during incubation and from 10 to 19 individuals during the nestling period.



Mass variation patterns between the sexes were also different in 1992. Females began incubation with a mean mass of  $33.8 \pm 0.5$  g ( $n = 15$ ) while males weighed  $30.5 \pm 0.4$  g ( $n = 11$ ), and there was a difference in mass between the sexes at this time ( $t = 5.14$ , d.f. = 24,  $p < 0.001$ ). While females lost an average of 0.13 g per day from the beginning of incubation to the end of the nestling period ( $t = 19.65$ ,  $p < 0.001$ ), males lost 0.04 g per day ( $t = 4.92$ ,  $p < 0.001$ ; Fig. 7). Again, males and females had different masses and lost mass at different rates (sex,  $F = 11.41$ , d.f. = 1, 53.45,  $p < 0.001$ ; sex\*day,  $F = 66.41$ , d.f. = 1, 673,  $p < 0.001$ ). At the end of the nestling stage, females had a mean mass of  $28.7 \pm 0.4$  g ( $n = 22$ ) and males weighed an average of  $29.3 \pm 0.3$  g ( $n = 17$ ). There was no difference in body mass between the sexes at this time ( $t = 1.13$ , d.f. = 37,  $p > 0.25$ ). Because male and female mass variation patterns were different in both years, the patterns for each sex were analyzed separately.

### Individual Differences

I tested for individual variation in 1991. In females, individuals had different masses and lost mass at different rates (bird,  $F = 5.12$ , d.f. = 22, 198,  $p < 0.001$ ; bird\*day,  $F = 2.58$ , d.f. = 22, 198,  $p < 0.001$ ; see Fig. 8). In males, individuals had different masses, however, individuals lost mass at the same rate (bird,  $F = 8.02$ , d.f. = 22, 232,  $p < 0.001$ ; bird\*day,  $F = 1.11$ , d.f. = 22, 232,  $p > 0.30$ ). For these reasons, I included individual bird in the ANCOVA models to account for this variation.

### Prelaying Masses

Data were not collected on prelaying birds in 1991. In 1992, prelaying females had an average mass of  $31.7 \pm 0.4$  g ( $n = 5$ ) whereas laying females had an average mass of  $34.1 \pm 0.7$  g ( $n = 5$ ). Prelaying females were lighter than laying females, although sample sizes were small (Paired t test,  $t = 3.40$ , d.f. = 4,  $p < 0.05$ ). Prelaying males had an average mass of  $30.0 \pm 0.8$  g ( $n = 9$ ) whereas during the laying stage males had an

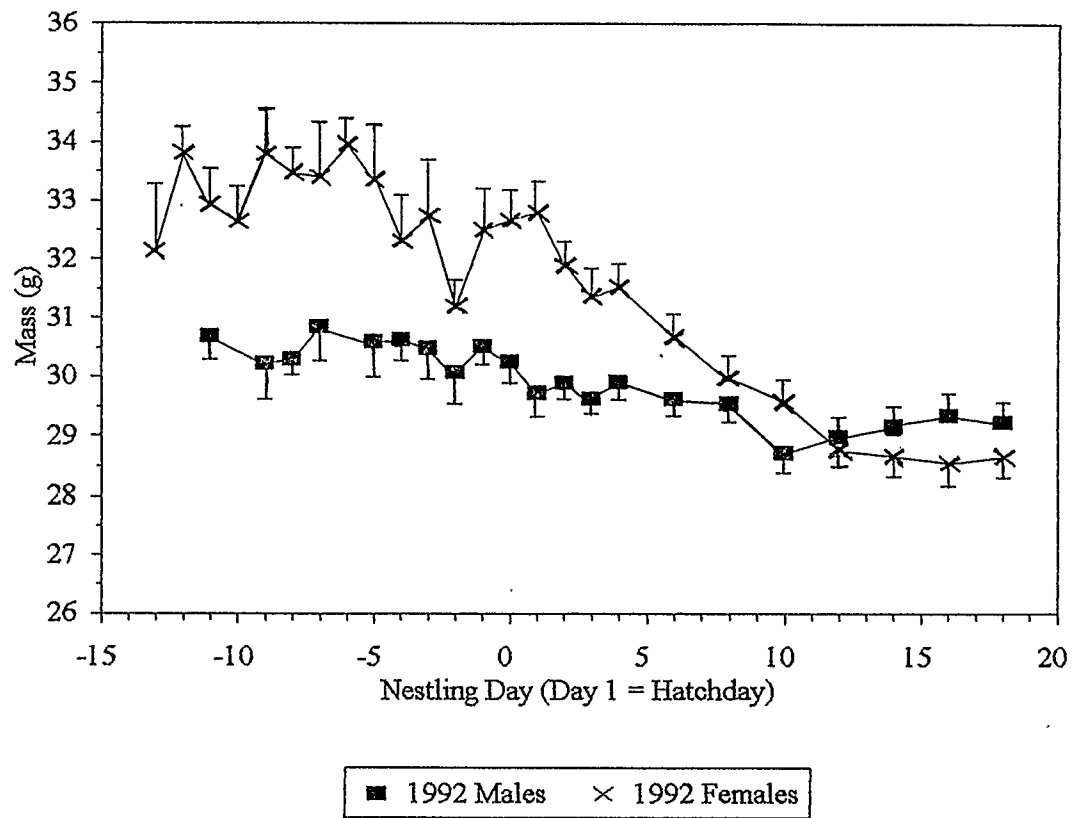


Fig. 7. Mass variation patterns in mean mass ( $\pm$  SE) by nestling day for males and females in 1992. Sample size ranged from 5 to 14 individuals during incubation and from 17 to 28 individuals during the nestling period.

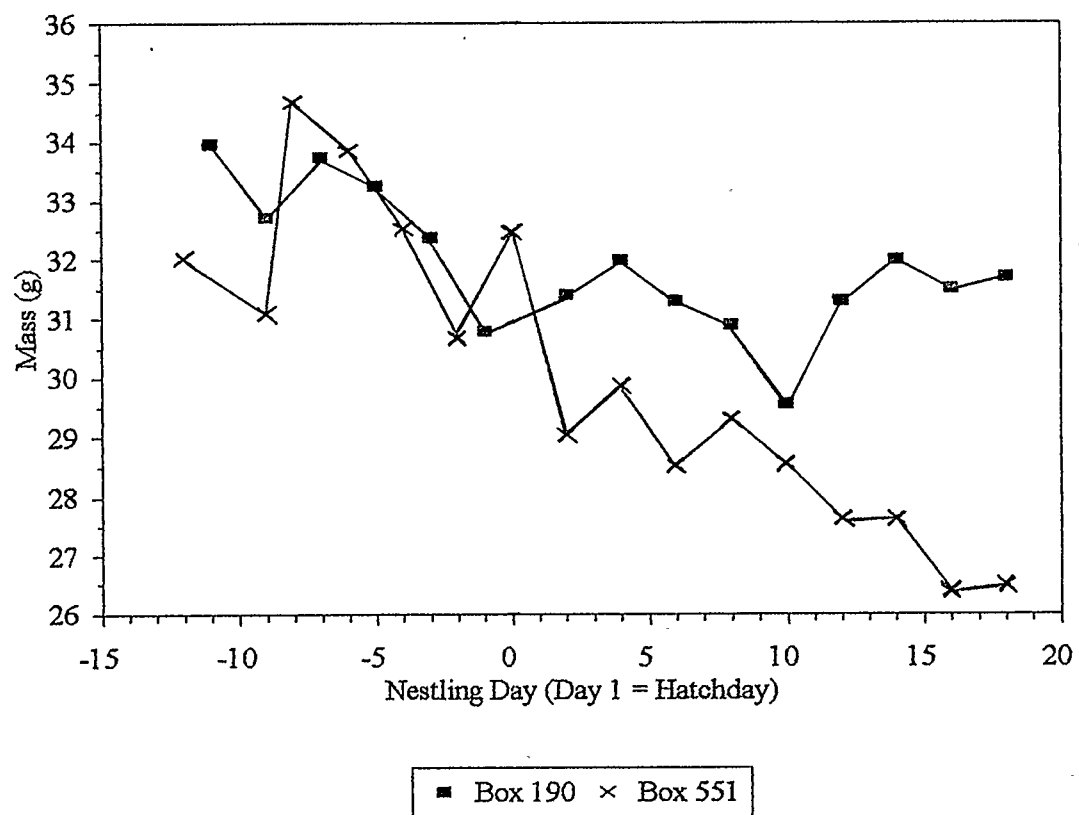


Fig. 8. Individual mass variation patterns for two females during the 1991 breeding season.

average mass of  $30.3 \pm 0.3$  g ( $n = 21$ ). Males weighed the same during prelaying and laying ( $t = 0.37$ , d.f. = 10,  $p > 0.70$ ). Thus, females increased body mass for breeding, while males did not.

### **Mass Variation During the Various Breeding Stages**

As I predicted for the flight adaptation hypothesis, females in both years lost mass in a decelerating pattern during the nestling stage (Fig. 6 and Fig. 7). In the regression model analyzing female mass loss during the nestling stage, DAY\*DAY was significantly negative indicating decelerating mass loss in both years (Table 5).

In females in both years and in males in 1992, the rate of mass change was different in the various reproductive stages. In 1991, females maintained mass during incubation ( $t = 1.31$ ,  $p > 0.15$ ), but lost mass during the hatch period (Inc 12 to ND 4; Single factor ANOVA,  $F = 5.07$ , d.f. = 3, 39,  $p < 0.005$ ) and during the nestling period ( $t = 5.37$ ,  $p < 0.001$ ; Fig. 6). Females had different masses in the various stages, and mass changed at different rates depending on stage (stage,  $F = 4.40$ , d.f. = 1, 92.28,  $p < 0.05$ ; stage\*day,  $F = 6.06$ , d.f. = 1, 192,  $p < 0.02$ ). Males in 1991 maintained mass during both incubation ( $t = 1.16$ ,  $p > 0.25$ ) and the nestling stage ( $t = 1.22$ ,  $p > 0.20$ ). However, males lost mass during the hatch period (Single factor ANOVA,  $F = 5.81$ , d.f. = 3, 39,  $p < 0.02$ ). Even so, males had the same mass, and mass changed at the same rate during both stages (stage,  $F = 1.27$ , d.f. = 1, 92.32,  $p > 0.25$ ; stage\*day,  $F = 1.23$ , d.f. = 1, 222,  $p > 0.25$ ).

In 1992, females maintained mass during incubation ( $t = 1.94$ ,  $p > 0.05$ ) and the hatch period (Single factor ANOVA,  $F = 1.51$ , d.f. = 6, 135,  $p > 0.15$ ), but lost mass during the nestling period ( $t = 4.25$ ,  $p < 0.001$ ; Fig. 7). Females had the same mass during the various stages, but they lost mass at different rates in the different stages (stage,  $F = 0.00$ , d.f. = 1, 56.06,  $p > 0.95$ ; stage\*day,  $F = 21.88$ , d.f. = 1, 364,  $p < 0.001$ ). Males maintained mass during incubation ( $t = 0.19$ ,  $p > 0.80$ ) and the hatch

Table 5. The equations of best fit for mass loss in adult females during the nestling period in 1991 and 1992. "Day" is the date within the nestling period.

| FEMALES       | BEST FIT EQUATION  | INTERCEPT                              | X TERM                                 | X <sup>2</sup> TERM                    |
|---------------|--|--|--|--|
| 1991 Controls | $32.91 - 0.33 \cdot \text{day} + 0.009 \cdot \text{day}^2$ | F = 3.30, d.f. = 22, 109,<br>p < 0.001 | F = 19.71, d.f. = 1, 109,<br>p < 0.001 | F = 4.30, d.f. = 1, 109,<br>p < 0.001  |
| 1992 Controls | $32.82 - 0.42 \cdot \text{day} + 0.011 \cdot \text{day}^2$ | F = 26.8, d.f. = 26, 245,<br>p < 0.001 | F = 98.29, d.f. = 1, 245,<br>p < 0.001 | F = 21.60, d.f. = 1, 245,<br>p < 0.001 |
| 1992 Exp.     | $33.51 - 0.49 \cdot \text{day} + 0.015 \cdot \text{day}^2$ | F = 7.79, d.f. = 19, 134,<br>p < 0.001 | F = 54.09, d.f. = 1, 134,<br>p < 0.001 | F = 18.26, d.f. = 1, 134,<br>p < 0.001 |

period (Single factor ANOVA,  $F = 0.84$ , d.f. = 6, 135,  $p > 0.50$ ), but lost mass during the nestling stage ( $t = 2.51$ ,  $p < 0.02$ ). Males had different masses in the various stages and lost mass at different rates in each stage (stage,  $F = 4.07$ , d.f. = 1, 58.15,  $p < 0.05$ ; stage\*day,  $F = 12.24$ , d.f. = 1, 256,  $p < 0.001$ ). Thus, both sexes in both years maintained mass during incubation. In 1991, both sexes lost mass during the hatch period, while in 1992 both sexes maintained mass during this period. Only males in 1991 maintained mass during the nestling stage. In both years and in both sexes, the patterns of mass variation were different during incubation and the nestling stage.

### **Effects of Clutch Size on Mass Variation**

In 1991, clutch size had no effect on mass variation in either females or males. Females with five-egg clutches lost an average of 0.16 g per day ( $t = 9.34$ ,  $p < 0.001$ ) during the nesting cycle, whereas females with six eggs lost 0.13 g per day ( $t = 7.58$ ,  $p < 0.001$ ). However, females with different clutch sizes had the same mass and lost mass at the same rate (clutch,  $F = 0.18$ , d.f. = 1, 23.58,  $p > 0.65$ ; clutch\*day,  $F = 1.76$ , d.f. = 1, 217,  $p > 0.15$ ). During incubation, females with five eggs lost an average of 0.10 g per day ( $t = 2.02$ ,  $p < 0.05$ ), while females with six eggs maintained mass ( $t = 0.74$ ,  $p > 0.45$ ). Again, females with different clutch sizes had the same mass and mass varied at the same rate (clutch,  $F = 1.50$ , d.f. = 1, 43.88,  $p > 0.20$ ; clutch\*day,  $F = 3.86$ , d.f. = 1, 100,  $p > 0.05$ ).

Males with five-egg clutches lost an average of 0.03 g per day ( $t = 2.69$ ,  $p < 0.01$ ) throughout the nesting cycle while males with clutches of six lost 0.02 g per day ( $t = 2.93$ ,  $p < 0.005$ ). Males had the same mass and lost mass at the same rate (clutch,  $F = 0.45$ , d.f. = 1, 23.04,  $p > 0.50$ ; clutch\*day,  $F = 0.07$ , d.f. = 1, 252,  $p > 0.75$ ). During incubation, males maintained mass regardless of clutch size (CS 5,  $t = 0.36$ ,  $p > 0.70$ ; CS 6,  $t = 1.34$ ,  $p > 0.15$ ). Males had the same mass and mass varied at the same rate

regardless of clutch size (clutch,  $F = 0.11$ , d.f. = 1, 44.13,  $p > 0.70$ ; clutch\*day,  $F = 1.07$ , d.f. = 1, 85,  $p > 0.30$ ).

In 1992, females with five-egg clutches lost an average 0.13 g per day ( $t = 11.59$ ,  $p < 0.001$ ) throughout the nesting cycle, while females with six eggs lost 0.14 g per day ( $t = 13.03$ ,  $p < 0.001$ ). Again, females with different clutch sizes had the same mass and lost mass at the same rate (clutch,  $F = 0.00$ , d.f. = 1, 25.48,  $p > 0.95$ ; clutch\*day,  $F = 1.22$ , d.f. = 1, 393,  $p > 0.25$ ). During incubation, clutch size had no effect on female mass, but there was an effect of clutch by day on female mass variation. Females with five eggs lost an average of 0.18 g per day ( $t = 5.21$ ,  $p < 0.001$ ), whereas females with six eggs maintained mass ( $t = 0.11$ ,  $p > 0.90$ ). Females with five eggs lost mass at a faster rate (clutch,  $F = 2.04$ , d.f. = 1, 22.69,  $p > 0.15$ ; clutch\*day,  $F = 11.82$ , d.f. = 1, 137,  $p < 0.001$ ). During the nestling stage, females with five-egg clutches lost an average of 0.20 g per day ( $t = 11.46$ ,  $p < 0.001$ ), whereas females with six eggs lost 0.25 g per day ( $t = 13.39$ ,  $p < 0.001$ ). Females with different clutch sizes had the same mass, but females with six eggs lost mass at a faster rate (clutch,  $F = 0.04$ , d.f. = 1, 30.37,  $p > 0.80$ ; clutch\*day,  $F = 4.40$ , d.f. = 1, 225,  $p < 0.05$ ).

In 1992, males with five-egg clutches lost an average of 0.05 g per day ( $t = 6.83$ ,  $p < 0.001$ ) throughout the nesting cycle, while males with six eggs lost 0.03 g per day ( $t = 2.62$ ,  $p < 0.01$ ). Males with different clutch sizes had the same mass, but males with five eggs lost mass at a faster rate (clutch,  $F = 0.00$ , d.f. = 1, 26.94,  $p > 0.95$ ; clutch\*day,  $F = 5.25$ , d.f. = 1, 277,  $p < 0.05$ ). During incubation, males with five eggs maintained mass ( $t = 0.74$ ,  $p > 0.45$ ), whereas males with six eggs gained 0.09 g per day ( $t = 2.35$ ,  $p < 0.02$ ). Again, males with different clutches had the same mass, but males with five eggs lost mass at a faster rate (clutch,  $F = 0.35$ , d.f. = 1, 24.11,  $p > 0.55$ ; clutch\*day,  $F = 6.97$ , d.f. = 1, 86,  $p < 0.01$ ). During the nestling stage, males with five eggs lost an average of 0.07 g per day ( $t = 5.12$ ,  $p < 0.001$ ), while males with six eggs lost 0.04 g per day ( $t = 2.70$ ,  $p < 0.01$ ). Males with different clutch sizes had the same

mass and lost mass at the same rate during the nestling period (clutch,  $F = 0.31$ , d.f. = 1, 32.69,  $p > 0.55$ ; clutch\*day,  $F = 1.88$ , d.f. = 1, 167,  $p > 0.15$ ). Because clutch size was not a significant factor affecting mass variation in 1991, it was not included in the ANCOVA models. However, clutch size was important in 1992, and it was included in 1992 models where appropriate.

### **Factors Affecting Second Brood Attempts**

Using 1991 data, I examined factors that might influence whether a pair would attempt a second brood. The amount of mass lost during the first attempt did not predict whether a female would initiate a second attempt. Females with second broods lost the same amount of mass in the first brood attempt as did females that did not have second broods ( $t = 1.75$ , d.f. = 5.1,  $p > 0.10$ ). In addition, female mass at the beginning (Inc 2) or at the end of the first attempt (ND 18) was not a reliable indicator of whether a second brood would be attempted (early mass,  $t = 0.28$ , d.f. = 10,  $p > 0.75$ ; late mass,  $t = 0.06$ , d.f. = 10,  $p > 0.95$ ). The only factor that influenced whether a female attempted a second brood was the hatch date of the first brood ( $t = 2.99$ , d.f. = 21,  $p < 0.01$ ). Females who initiated their first broods early in the season were more likely to attempt a second brood than females who started their first broods later in the season.

### **Differences Between First and Second Broods**

Patterns of mass variation of adults during the first brood attempt and the second attempt were compared in each year. In 1991, there was a difference in female mass but not the rate of mass loss between the first brood attempt and the second (brood,  $F = 5.06$ , d.f. = 1, 27.81,  $p < 0.05$ ; brood\*day,  $F = 0.12$ , d.f. = 1, 269,  $p > 0.70$ ). Females began the second brood attempt about 1.5 g lighter than they did the first. When the various stages were examined alone, there was no difference in female mass or the rate of mass loss between the two attempts during incubation (brood,  $F = 0.30$ , d.f. = 1,



51.18,  $p > 0.55$ ; brood\*day,  $F = 1.66$ , d.f. = 1, 122,  $p > 0.20$ ) or the nestling stage (brood,  $F = 0.39$ , d.f. = 1, 44.21,  $p > 0.50$ ; brood\*day,  $F = 3.27$ , d.f. = 1, 114,  $p > 0.05$ ). Females had the same mass at the end of the nesting cycle regardless of the brood attempt ( $t = 0.02$ , d.f. = 19,  $p > 0.95$ ).

In 1991 males, there was no difference in mass between the first brood attempt and the second. However, males lost mass at a faster rate during the first attempt (brood,  $F = 0.02$ , d.f. = 1, 27.33,  $p > 0.90$ ; brood\*day,  $F = 6.38$ , d.f. = 1, 299,  $p < 0.02$ ). There was no difference in mass or the rate of mass change between the two brood attempts during either incubation (brood,  $F = 0.00$ , d.f. = 1, 48.56,  $p > 0.95$ ; brood\*day,  $F = 0.10$ , d.f. = 1, 106,  $p > 0.75$ ) or the nestling period (brood,  $F = 0.00$ , d.f. = 1, 62.18,  $p > 0.95$ , brood\*day,  $F = 0.01$ , d.f. = 1, 150,  $p > 0.90$ ). Males had the same mass at the end of the nesting cycle regardless of the brood attempt ( $t = 1.32$ , d.f. = 16,  $p > 0.20$ ). Thus, for both sexes in 1991, the only difference in mass variation between broods was seen when the entire nesting cycle was examined. Females were lighter for the second breeding attempt but lost mass at a similar rate in both attempts. Males had the same mass for both breeding attempts but lost mass faster during the first breeding attempt.

In 1992, there was no difference in either female mass or the rate of mass loss throughout the nesting cycle in the two attempts (brood,  $F = 2.80$ , d.f. = 1, 34.09,  $p > 0.10$ ; brood\*day,  $F = 1.35$ , d.f. = 1, 467,  $p > 0.20$ ). In addition, there was no difference in female mass or the rate of mass loss during incubation (brood,  $F = 1.54$ , d.f. = 1, 34.09,  $p > 0.20$ ; brood\*day,  $F = 1.25$ , d.f. = 1, 167,  $p > 0.25$ ). However, during the nestling stage, females were heavier and lost mass at a faster rate during the first brood attempt (brood,  $F = 7.67$ , d.f. = 1, 42.67,  $p < 0.01$ ; brood\*day,  $F = 6.11$ , d.f. = 1, 262,  $p < 0.02$ ). Females had the same mass at the end of the nesting cycle regardless of the brood attempt ( $t = 0.44$ , d.f. = 24,  $p > 0.65$ ).

In 1992, male mass was the same for both brood attempts. However, males in the first attempt lost mass at a faster rate than did males in the second attempt (brood,  $F = 0.21$ , d.f. = 1, 28.08,  $p > 0.65$ ; brood\*day,  $F = 11.64$ , d.f. = 1, 308,  $p < 0.001$ ). During incubation, males in both brood attempts had the same mass and the same rate of mass change (brood,  $F = 0.02$ , d.f. = 1, 27.13,  $p > 0.90$ ; brood\*day,  $F = 0.97$ , d.f. = 1, 98,  $p > 0.30$ ). During the nestling period, males had the same mass in both attempts but lost mass at a faster rate in the first brood attempt (brood,  $F = 1.30$ , d.f. = 1, 32.59,  $p > 0.25$ ; brood\*day,  $F = 11.57$ , d.f. = 1, 182,  $p < 0.001$ ). Males had the same mass at the end of the nesting cycle regardless of the brood attempt ( $t = 1.80$ , d.f. = 22,  $p > 0.08$ ). Thus, in 1992, females in the first attempt were heavier, and they lost mass at a faster rate during the nestling stage. Males in the first attempt lost mass faster both overall and during the nestling stage. Since there was an effect of brood attempt on adult mass variation patterns, each brood attempt was analyzed separately in the analyses of year to year variation and the food supplementation experiment.

### **Variation Resulting from Brood Size**

Using 1991 data, the effect of brood size on adult mass variation was examined. During the nestling stage, females with broods of four lost an average of 0.16 g per day ( $t = 2.80$ ,  $p < 0.01$ ), females with five young maintained mass ( $t = 1.82$ ,  $p > 0.07$ ), and females with six young lost 0.19 g per day ( $t = 3.98$ ,  $p < 0.001$ ). However, there was no effect of brood size on either mass or the rate of mass loss (young,  $F = 1.93$ , d.f. = 2, 57.54,  $p > 0.15$ ; young\*day,  $F = 1.90$ , d.f. = 2, 81,  $p > 0.15$ ). Males maintained mass regardless of brood size (BS 4,  $t = 0.86$ ,  $p > 0.35$ ; BS 5,  $t = 0.67$ ,  $p > 0.50$ ; BS 6,  $t = 0.05$ ,  $p > 0.95$ ). There was no difference in male mass or the rate of mass loss due to the number of young in the nest (young,  $F = 0.32$ , d.f. = 2, 41.97,  $p > 0.80$ ; young\*day,  $F = 0.77$ , d.f. = 2, 131,  $p > 0.55$ ). Thus, brood size did not affect adult mass or the rate of mass loss and was not incorporated into further analyses.

### **Variation in the Pattern of Mass Change Resulting from Adult Age**

From the Ellis Bird Farm banding records, I obtained age data on a small portion of the adults in the population. Individuals were aged from known hatch dates, or if this was not possible, minimum age was determined using the earliest year that the individual was seen on the study area. For 1991, I obtained the ages of 19 males and 14 females. For 1992, I obtained the ages for 29 males and 28 females. Most of these data were minimum ages because few banded young return to the study area as adults. Age had no effect on clutch size in either sex in either year (age,  $F \leq 0.30$ , d.f.  $\geq 1$ , 13,  $p > 0.55$  in all cases; age\*egg1date,  $F \leq 0.36$ , d.f.  $\geq 1$ , 13,  $p > 0.55$  in all cases). Date of the first egg was included in the model because clutch size in passerines often decreases later in the breeding season (Haukioja 1970; Hussell 1972; Jarvinen and Linden 1980; Stutchbury and Robertson 1988). Age also had no effect on the number of young fledged in either sex in either year (age,  $F \leq 1.97$ , d.f.  $\geq 1$ , 4,  $p > 0.15$ ; age\*egg1date,  $F \leq 2.13$ , d.f.  $\geq 1$ , 4,  $p > 0.15$ , in all cases). Thus, older, and perhaps more-experienced, birds did not have larger clutch sizes, nor did they fledge more young.

Percent mass loss from Inc 2 to ND 18 was then calculated by dividing the amount lost in that period by the mass on Inc 2. There was no effect of age on percent mass loss during the nesting cycle for either sex in 1991 (Single factor ANOVA, females,  $F = 0.86$ , d.f. = 1, 12,  $p > 0.35$ ; males,  $F = 0.12$ , d.f. = 1, 16,  $p > 0.70$ ). There was also no effect of age on percent mass loss in 1992 control pairs (females,  $F = 0.02$ , d.f. = 1, 10,  $p > 0.85$ ; males,  $F = 0.01$ , d.f. = 1, 5,  $p > 0.90$ ), or supplemented pairs (females,  $F = 0.14$ , d.f. = 1, 7,  $p > 0.70$ ; males,  $F = 4.54$ , d.f. = 1, 9,  $p > 0.07$ ). Thus, older birds lost the same amount of mass as did younger birds.

## YEAR TO YEAR VARIATION

### Life History Traits

I compared life history traits between years to control for factors that may have affected the patterns of adult mass variation. In 1991, the mean clutch size was  $5.5 \pm 0.1$  eggs ( $n = 23$ ), while the mean clutch size in 1992 was  $5.5 \pm 0.1$  eggs ( $n = 25$ ). Clutch size was not different between years ( $t = 0.28$ , d.f. = 46,  $p > 0.75$ ). In 1991, the mean brood size was  $5.0 \pm 0.2$  young ( $n = 23$ ), while in 1992 the mean brood size was  $4.9 \pm 0.2$  young ( $n = 25$ ). There was no difference in brood size between years ( $t = 0.13$ , d.f. = 46,  $p > 0.85$ ). In 1991, the mean first egg date was  $131.4 \pm 0.2$  days (May 11,  $n = 23$ ), while in 1992 the mean first egg date was  $132.7 \pm 0.3$  days (May 11,  $n = 21$ ; 1992 was a leap year and therefore different Julian dates result in the same calendar date here). There was no difference in the date of the first egg between years ( $t = 0.44$ , d.f. = 42,  $p > 0.65$ ). The mean hatch date in 1991 was  $150.0 \pm 0.2$  days (May 30,  $n = 23$ ), while the mean hatch date in 1992 was  $154.4 \pm 0.1$  days (June 2,  $n = 25$ ). Mean hatch dates were similar in both years ( $t = 1.45$ , d.f. = 46,  $p > 0.15$ ).

### Adult Females

#### First Broods

In 1991, females began incubation at a mean mass of  $35.2 \pm 0.6$  g ( $n = 8$ ) whereas 1992 females weighed  $33.8 \pm 0.5$  g ( $n = 15$ ). There was no difference in mass between years ( $t = 1.91$ , d.f. = 26,  $p > 0.06$ ). Throughout the nesting cycle, females in 1991 lost an average of 0.15 g per day ( $t = 13.14$ ,  $p < 0.001$ ) while females in 1992 lost 0.13 g per day ( $t = 16.52$ ,  $p < 0.001$ ; Fig. 9). Females had the same mass and lost mass at the same rate (year,  $F = 2.95$ , d.f. = 1, 49.40,  $p > 0.09$ ; year\*day,  $F = 1.07$ , d.f. = 1, 614,  $p > 0.30$ ).

When the nesting cycle was separated into the incubation and nestling stages, incubating females maintained mass in 1991 ( $t = 1.30$ ,  $p > 0.15$ ) whereas females lost an

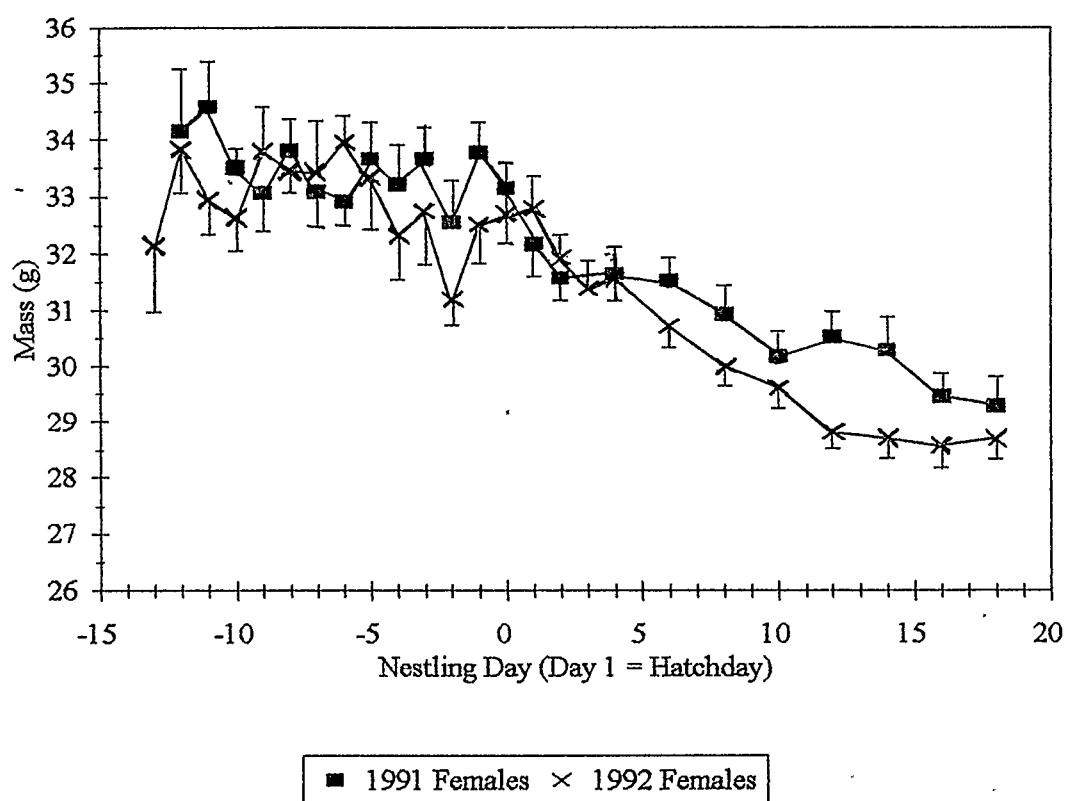


Fig. 9. Mass variation patterns in mean mass ( $\pm$  SE) per nestling day for females during the 1991 and 1992 first brood attempt. Sample sizes ranged from 5 to 14 individuals during incubation and from 10 to 28 individuals during the nestling period.

average of 0.10 g per day in 1992 ( $t = 3.61$ ,  $p < 0.001$ ). Again, females had the same mass and mass changed at the same rate in both years (year,  $F = 1.55$ , d.f. = 1, 56.1,  $p > 0.20$ ; year\*day,  $F = 2.01$ , d.f. = 1, 240,  $p > 0.15$ ). Incubation lasted  $15.1 \pm 0.2$  days in 1991 ( $n = 23$ ) and  $15.4 \pm 0.3$  days in 1992 ( $n = 22$ ;  $t = 0.73$ , d.f. = 43,  $p > 0.45$ ).

During the nestling stage, females lost an average of 0.14 g per day in 1991 ( $t = 6.66$ ,  $p < 0.001$ ), whereas females in 1992 lost 0.23 g per day ( $t = 17.02$ ,  $p < 0.001$ ). There was no difference in the pattern of mass loss between females in 1991 and females in 1992 (Table 6). Females had the same mass at the end of the nesting cycle in both years. On ND 18, females had a mean mass of  $29.1 \pm 0.5$  g ( $n = 16$ ) in 1991 and a mean mass of  $28.7 \pm 0.4$  g ( $n = 22$ ) in 1992 ( $t = 0.70$ , d.f. = 36,  $p > 0.45$ ).

The energetic needs of the nestlings change from the time of hatching to fledging. To determine whether mass loss corresponded to the most "stressful period", the nestling stage was separated into three phases, early (ND 1 to ND 6), middle (ND 7 to ND 12), and late (ND 13 to ND 18). During the early nestling phase, the female alone broods the young. In 1991, females maintained mass during this phase ( $t = 0.83$ ,  $p > 0.40$ ) while females in 1992 lost an average of 0.30 g per day ( $t = 4.84$ ,  $p < 0.001$ ). However, statistically, females had the same mass, and mass changed at the same rate in both years (year,  $F = 1.71$ , d.f. = 1, 117.22,  $p > 0.15$ ; year\*day,  $F = 3.82$ , d.f. = 1, 117,  $p > 0.05$ ).

The nestlings show rapid growth during the mid nestling period from ND 7 to ND 12, and nestling energetic demands increase rapidly at this time (Mock et al. 1991; Garcia et al., in review; this study). During this phase, females maintained mass in 1991 ( $t = 0.22$ ,  $p > 0.80$ ) whereas females in 1992 lost an average of 0.30 g per day ( $t = 4.26$ ,  $p < 0.001$ ). Females had the same mass in both years, but lost mass at a faster rate in 1992 (year,  $F = 1.63$ , d.f. = 1, 74.81,  $p > 0.20$ ; year\*day,  $F = 5.46$ , d.f. = 1, 62,  $p < 0.02$ ).

By ND 13, the nestlings are approximately adult mass, and their energetic needs show little day to day change (Mock et al. 1991; this study). During this phase, females

Table 6. Comparison of the patterns of mass loss by females in 1991 and 1992 during the nestling period using a Mixed-model Analysis of Covariance (ANCOVA). Individual bird is a random variable in the model, and day is the day within the nestling period.

| VARIABLE     | F VALUE   | DEGREES OF FREEDOM | P         |
|--------------|-----------|--------------------|-----------|
| Year         | F = 0.69  | d.f. = 1, 76.23    | p > 0.40  |
| Bird(Year)   | F = 13.15 | d.f. = 48, 373     | p < 0.001 |
| Day          | F = 75.95 | d.f. = 1, 373      | p < 0.001 |
| Day*Year     | F = 0.04  | d.f. = 1, 373      | p > 0.80  |
| Day*Day      | F = 13.17 | d.f. = 1, 373      | p < 0.001 |
| Day*Day*Year | F = 0.12  | d.f. = 1, 373      | p > 0.70  |

maintained mass in both years (1991,  $t = 0.13$ ,  $p > 0.85$ ; 1992,  $t = 1.09$ ,  $p > 0.25$ ).

Females had the same mass and mass varied at the same rate in both years (year,  $F = 0.01$ , d.f. = 1, 51.27,  $p > 0.90$ ; year\*day,  $F = 0.06$ , d.f. = 1, 48,  $p > 0.80$ ). Thus, the differences in the pattern of mass variation between years were primarily due to a greater rate of mass loss by 1992 females during the first two-thirds of the nestling stage.

### Second Broods

Similar patterns were evident in the second brood attempt. In 1991, females began incubation with a mean mass of  $31.2 \pm 0.3$  g ( $n = 5$ ) while females in 1992 weighed  $31.9 \pm 0.6$  g ( $n = 6$ ). Overall, females in 1991 lost an average of 0.15 g per day ( $t = 10.18$ ,  $p < 0.001$ ), while females in 1992 lost 0.14 g per day ( $t = 11.52$ ,  $p < 0.001$ ; Fig. 10). As in the first breeding attempt, females had the same mass and lost mass at the same rate in both years (year,  $F = 1.01$ , d.f. = 1, 14.17,  $p > 0.30$ ; year\*day,  $F = 0.02$ , d.f. = 1, 216,  $p > 0.90$ ). Females in both years maintained mass during incubation (1991,  $t = 1.26$ ,  $p > 0.20$ ; 1992,  $t = 1.50$ ,  $p > 0.10$ ). While incubating females were slightly heavier in 1991, female mass varied at the same rate in both years (year,  $F = 4.33$ , d.f. = 1, 21.24,  $p < 0.05$ ; year\*day,  $F = 3.74$ , d.f. = 1, 83,  $p > 0.05$ ). Finally, during the nestling stage, females in 1991 lost an average of 0.21 g per day ( $t = 6.12$ ,  $p < 0.001$ ), and females in 1992 lost 0.16 g per day ( $t = 6.63$ ,  $p < 0.001$ ). Females had the same mass and lost mass at the same rate (year,  $F = 1.38$ , d.f. = 1, 22.81,  $p > 0.25$ ; year\*day,  $F = 1.62$ , d.f. = 1, 112,  $p > 0.20$ ). At the end of the second nestling period, there was no significant difference in female mass between 1991 ( $29.1 \pm 0.6$  g,  $n = 5$ ) and 1992 ( $28.5 \pm 0.4$  g,  $n = 6$ ;  $t = 0.91$ , d.f. = 9,  $p > 0.35$ ).

In summary, females had similar body-mass dynamics in both years. Females in 1991 began incubation at 35.2 g, while in 1992 females weighed 33.8 g. Females had the same mass and mass varied at the same rate during incubation. Females lost mass during the nestling stage in both years, but in 1992 they lost mass at a faster rate, particularly



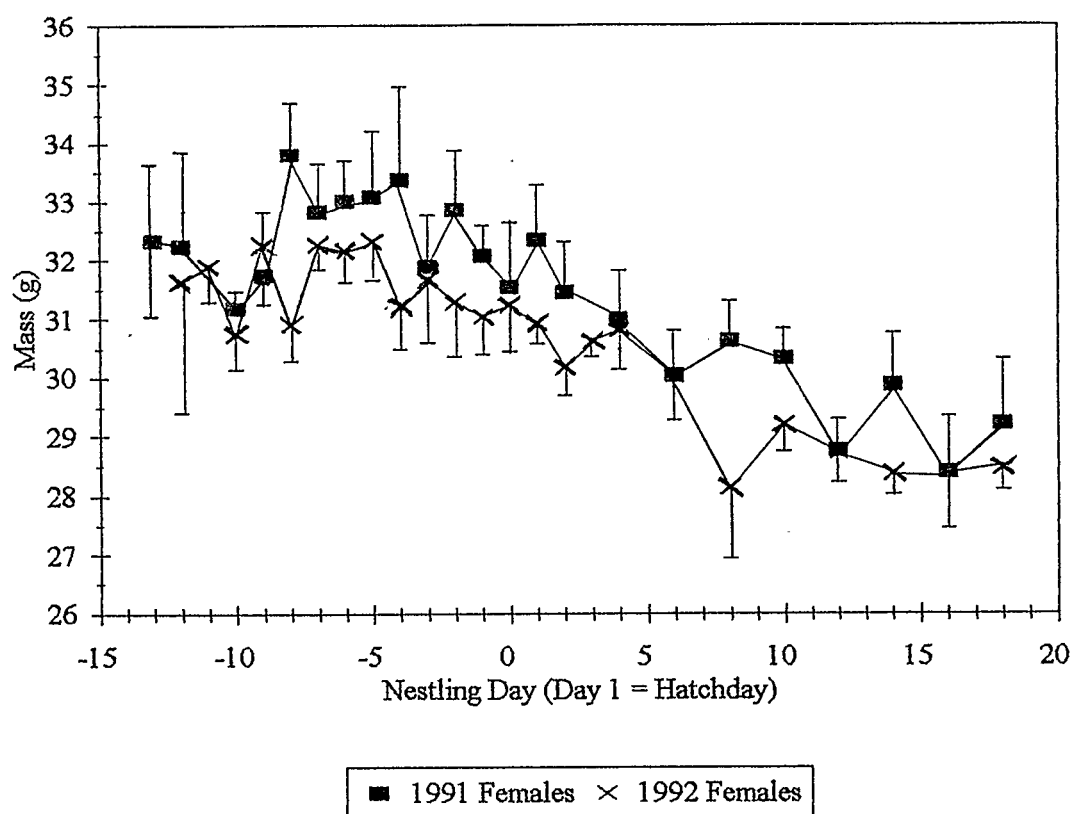


Fig. 10 Mass variation patterns in mean mass ( $\pm$  SE) per nestling day for 1991 and 1992 females during the second brood attempt. Sample sizes ranged from 2 to 5 individuals during incubation and from 3 to 8 individuals during the nestling period.

during the mid nestling period. From Inc 2 to ND 18, females in 1991 lost about 5.1 g in total, or close to 14 % of their initial body mass, and females in 1992 lost 4.7 g in total, or about 14 % of their body mass.

In the second brood attempt, females also had similar body mass dynamics in the two years. Females began incubation at the same mass, although females in 1991 were generally heavier during the incubation stage. In both years, females maintained mass during incubation and lost mass at the same rate during the nestling stage. From Inc 2 to ND 18, females in 1991 lost 2 g in total or about 6 % of their initial body mass, while females in 1992 lost 3.4 g in total or close to 11 % of their body mass.

## **Adult Males**

### **First Broods**

In 1991, males began incubation at a mean mass of  $29.5 \pm 0.4$  g ( $n = 6$ ), while males in 1992 weighed  $30.3 \pm 0.3$  g ( $n = 21$ ), and there was no difference in mass ( $t = 1.29$ , d.f. = 25,  $p > 0.20$ ). Throughout the nesting cycle, males in 1991 lost an average of 0.03 g per day ( $t = 4.48$ ,  $p < 0.001$ ) while in 1992 males lost 0.04 g per day ( $t = 6.49$ ,  $p < 0.001$ ; Fig. 11). Males had the same mass and lost mass at the same rate in both years (year,  $F = 0.09$ , d.f. = 1, 49.35,  $p > 0.75$ ; year\*day,  $F = 2.83$ , d.f. = 1, 533,  $p > 0.09$ ).

When the nesting cycle was separated into incubation and the nestling stage, males maintained mass during incubation in both years (1991,  $t = 0.11$ ,  $p > 0.90$ ; 1992,  $t = 0.73$ ,  $p > 0.45$ ), and males had the same mass and lost mass at the same rate (year,  $F = 1.50$ , d.f. = 1, 57.73,  $p > 0.20$ ; year\*day,  $F = 0.24$ , d.f. = 1, 174,  $p > 0.60$ ). During the nestling stage, males maintained mass in 1991 ( $t = 1.56$ ,  $p > 0.10$ ), and lost an average of 0.06 g per day in 1992 ( $t = 4.68$ ,  $p < 0.001$ ). Again, males had the same mass and mass varied at the same rate in both years (year,  $F = 0.25$ , d.f. = 1, 67.09,  $p > 0.60$ ; year\*day,  $F = 3.71$ , d.f. = 1, 296,  $p > 0.05$ ).

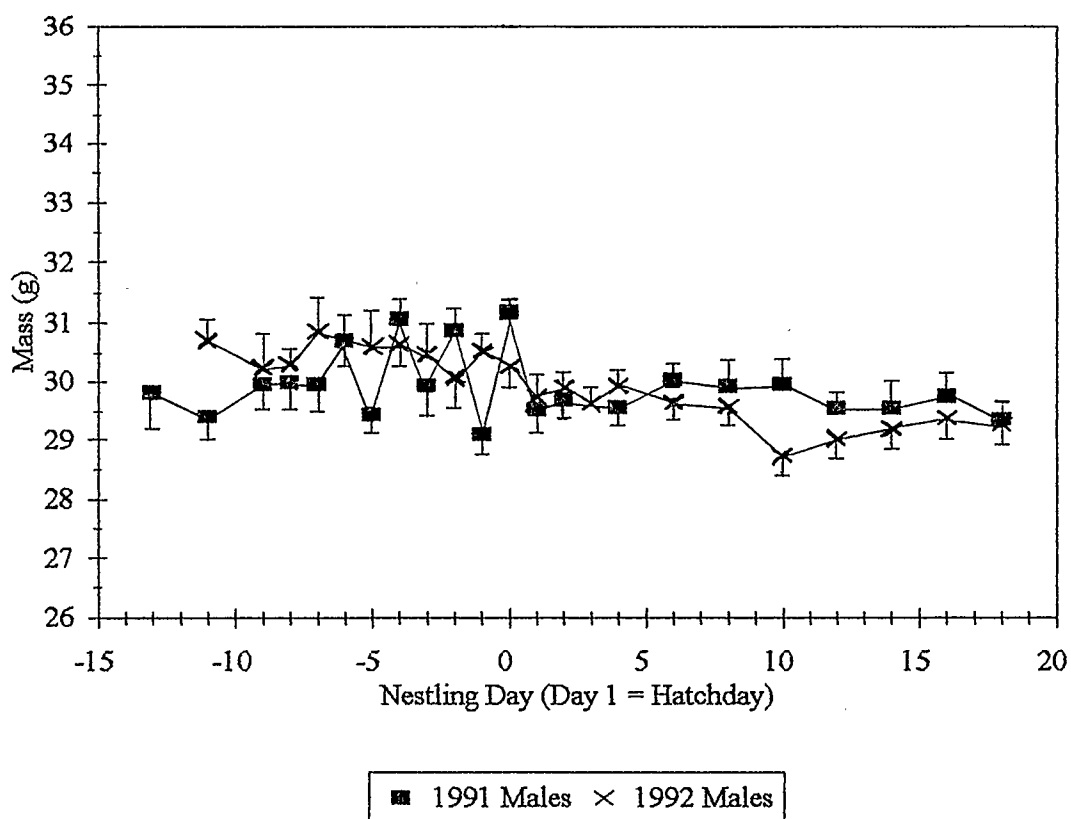


Fig. 11. Mass variation patterns in mean mass ( $\pm$  SE) per nestling day for males during the 1991 and 1992 first brood attempt. Sample sizes ranged from 5 to 14 during incubation and from 10 to 28 during the nestling period.

When the nestling stage was separated into three phases, males maintained mass during the early nestling phase in both years (1991,  $t = 1.22$ ,  $p > 0.20$ ; 1992,  $t = 1.97$ ,  $p > 0.05$ ). Males had the same mass in both years. However, males in 1992 lost mass at a faster rate than males in 1991 (year,  $F = 1.88$ , d.f. = 1, 97.76,  $p > 0.15$ ; year\*day,  $F = 4.92$ , d.f. = 1, 101,  $p < 0.05$ ). During the mid nestling phase, males also maintained mass in both years (1991,  $t = 1.59$ ,  $p > 0.10$ ; 1992,  $t = 1.34$ ,  $p > 0.15$ ). Males had the same mass, and mass changed at the same rate (year,  $F = 0.37$ , d.f. = 1, 70.78,  $p > 0.50$ ; year\*day,  $F = 0.07$ , d.f. = 1, 59,  $p > 0.75$ ). During the late nestling phase, males maintained mass in both years (1991,  $t = 1.22$ ,  $p > 0.20$ ; 1992,  $t = 0.31$ ,  $p > 0.75$ ). Again, there was no effect of year or year\*day on male mass variation (year,  $F = 1.73$ , d.f. = 1, 59.66,  $p > 0.15$ ; year\*day,  $F = 1.30$ , d.f. = 1, 55,  $p > 0.25$ ). Thus, males in 1992 lost mass at a faster rate than males in 1991 only during the early nestling phase.

## Second Broods

In 1991, males began the second brood attempt with a mean mass of  $30.3 \pm 0.9$  g ( $n = 7$ ) while males in 1992 weighed  $30.6 \pm 0.5$  g ( $n = 4$ ). In both years, males maintained mass throughout the nesting cycle (1991,  $t = 0.39$ ,  $p > 0.65$ ; 1992,  $t = 0.58$ ,  $p > 0.55$ ; Fig. 12). Males had the same mass and mass varied at the same rate in both years (year,  $F = 0.40$ , d.f. = 1, 12.08,  $p > 0.50$ ; year\*day,  $F = 0.48$ , d.f. = 1, 170,  $p > 0.40$ ). In both years, males maintained mass during incubation (1991,  $t = 0.84$ ,  $p > 0.40$ ; 1992,  $t = 0.68$ ,  $p > 0.45$ ) and the nestling period (1991,  $t = 0.95$ ,  $p > 0.30$ ; 1992,  $t = 1.22$ ,  $p > 0.20$ ), and there was no effect of year or year\*day on mass variation in either stage (Incubation: year,  $F = 0.17$ , d.f. = 1, 13.97,  $p > 0.60$ ; year\*day,  $F = 0.00$ , d.f. = 1, 63,  $p > 0.95$ ; Nestling stage: year,  $F = 0.86$ , d.f. = 1, 17.05,  $p > 0.30$ ; year\*day,  $F = 0.00$ , d.f. = 1, 84,  $p > 0.10$ ). At the end of the nestling stage, males in 1991 had a mean mass of  $30.3 \pm 0.8$  g ( $n = 4$ ) and males in 1992 weighed  $30.4 \pm 0.3$  g ( $n = 6$ ;  $t = 0.12$ , d.f. = 8,  $p$

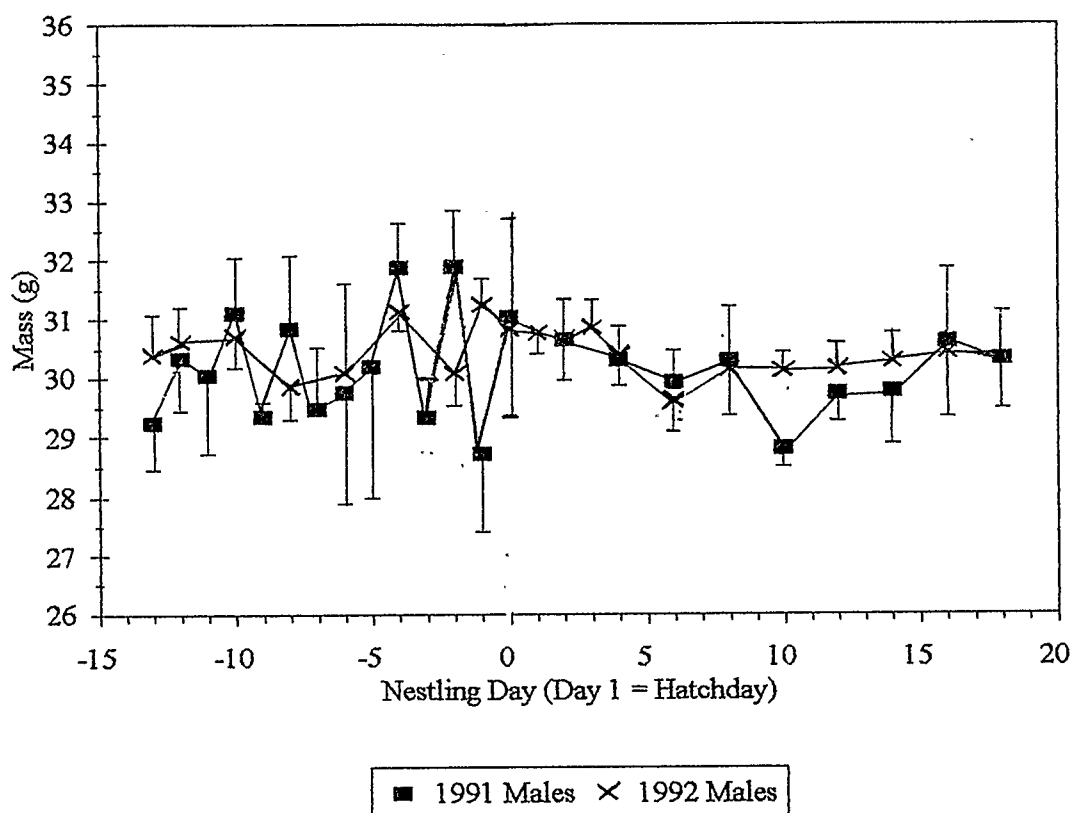


Fig. 12. Mass variation patterns in mean mass ( $\pm$  SE) per nestling day for 1991 and 1992 males during the second brood attempt. Sample sizes ranged from 2 to 5 individuals during incubation and from 3 to 8 individuals during the nestling period.

> 0.90). Thus, the pattern of male mass variation during the second brood attempt was similar in both years.

In summary, males had similar body-mass dynamics in the two years. Males began the incubation period at the same mass, and there was no difference in mass variation between years either throughout the nesting cycle or during incubation. Male mass varied at the same rate during the nestling stage in both years. However, early in the nestling stage, while females were brooding, males lost mass at a faster rate in 1992 than in 1991. From the beginning of incubation to the end of the nestling stage, males in 1991 maintained mass, while males in 1992 lost 1.4 g or close to 5 % of their initial body mass. In the second brood attempt there was no difference in male mass variation between the two years at any time.

### **Nestlings**

On ND 6, nestlings in 1992 were lighter and smaller than nestlings in 1991 (mass,  $t = 5.42$ , d.f. = 233,  $p < 0.001$ ; tarsus,  $t = 3.83$ , d.f. = 233,  $p < 0.001$ ; Figs. 4 and 5). On ND 12 and ND 18, nestlings in 1992 were lighter than 1991 nestlings. However, there was no difference in tarsus length (ND 12: mass,  $t = 6.93$ , d.f. = 188.6,  $p < 0.001$ ; tarsus,  $t = 1.32$ , d.f. = 188.6,  $p > 0.15$ ; ND 18: mass,  $t = 2.18$ , d.f. = 164.8,  $p < 0.05$ ; tarsus,  $t = 0.92$ , d.f. = 141.6,  $p > 0.35$ ). Thus, at all three nestling phases, 1992 nestlings were lighter than 1991 nestlings. In addition, nestlings had smaller tarsi on ND 6 in 1992 than in 1991.

Similar patterns were seen in nestling growth patterns in the second broods. On ND 6, 1991 nestlings had a mean mass of  $14.9 \pm 0.6$  g ( $n = 30$ ) and a mean tarsus of  $15.5 \pm 0.4$  mm ( $n = 30$ ). Nestlings in 1992 had a mean mass of  $12.0 \pm 0.4$  g ( $n = 34$ ) and a mean tarsus of  $13.5 \pm 0.3$  mm ( $n = 34$ ). Nestlings in 1992 were lighter and had smaller tarsi than 1991 nestlings (mass,  $t = 4.41$ , d.f. = 48.4,  $p < 0.001$ ; tarsus,  $t = 4.67$ , d.f. = 62,  $p < 0.001$ ). On ND 12, 1991 nestlings had a mean mass of  $27.3 \pm 0.4$  g ( $n = 29$ ) and

a mean tarsus of  $23 \pm 0.2$  mm ( $n = 29$ ). Nestlings in 1992 weighed  $25.6 \pm 0.4$  g ( $n = 31$ ) and had a mean tarsus of  $22.7 \pm 0.2$  mm ( $n = 31$ ). There was a difference in mass, but not in tarsus length (mass,  $t = 2.88$ , d.f. = 58,  $p < 0.005$ ; tarsus,  $t = 1.29$ , d.f. = 58,  $p > 0.20$ ). On ND 18, 1991 nestlings had a mean mass of  $27.8 \pm 0.4$  g ( $n = 16$ ) and a mean tarsus of  $23.2 \pm 0.2$  mm ( $n = 16$ ). Nestlings in 1992 weighed  $27.4 \pm 0.4$  g ( $n = 24$ ) and had a mean tarsus of  $23.3 \pm 0.2$  mm ( $n = 24$ ). There was no difference in either mass or tarsus (mass,  $t = 0.60$ , d.f. = 38,  $p > 0.50$ ; tarsus,  $t = 0.26$ , d.f. = 38,  $p > 0.75$ ). Thus, in second broods, 1991 nestlings grew faster, but there was no difference in mass or tarsus at the time of fledging.

In 1991, three out of 117 (3 %) nestlings died, all prior to ND 6, presumably due to starvation. In 1992, 11 out of 134 (8 %) nestlings died prior to fledging. Most of these nestlings died prior to ND 6, although one died after ND 12. Again, the cause of death was presumed to be starvation. Of the 11, nine from two nest boxes died of starvation and/or hypothermia during the two-day snowstorm with below freezing temperatures in mid-May.

## **Time Activity Budgets**

### **Females**

During early incubation (Inc 5), females did not differ in the amount of time spent flying, sitting, or incubating between years (fly,  $t = 0.50$ , d.f. = 21,  $p > 0.60$ ; sit,  $t = 0.03$ , d.f. = 19.1,  $p > 0.95$ ; inc,  $t = 0.11$ , d.f. = 19.6,  $p > 0.90$ ; Table 3). During late incubation (Inc 10), 1992 females flew and incubated the same amounts of time as 1991 females but sat less (fly,  $t = 1.41$ , d.f. = 22,  $p > 0.15$ ; sit,  $t = 2.15$ , d.f. = 22,  $p < 0.05$ ; inc,  $t = 1.72$ , d.f. = 22,  $p > 0.09$ ). During the early nestling stage (ND 3), females in 1992 flew the same amounts of time as in 1991 females but sat less and brooded the young more (fly,  $t = 0.36$ , d.f. = 17,  $p > 0.70$ ; sit,  $t = 2.71$ , d.f. = 23,  $p < 0.02$ ; inc,  $t = 2.82$ , d.f. = 23,  $p < 0.01$ ). During the mid and late nestling periods (ND 10 and ND 18), females in 1992

flew more and sat less than did 1991 females (ND 10, fly,  $t = 2.65$ , d.f. = 20,  $p < 0.02$ ; sit,  $t = 2.81$ , d.f. = 20,  $p < 0.01$ ; ND 18, fly,  $t = 4.38$ , d.f. = 20,  $p < 0.001$ ; sit,  $t = 4.27$ , d.f. = 20,  $p < 0.001$ ). Thus, females in 1992 flew more than did females in 1991 during the mid and late nestling stages, sat less than females in 1991 during late incubation and all three nestling stages, and brooded the young more in the early nestling stage. Thus, females in 1992 worked harder during the nestling stage.

## Males

During early incubation, males in 1992 flew and sat for the same proportion of time as did males in 1991 (fly,  $t = 1.30$ , d.f. = 17.1,  $p > 0.20$ ; sit,  $t = 1.21$ , d.f. = 17,  $p > 0.20$ ; Table 3). During late incubation, 1992 males flew more and sat less than 1991 males (fly,  $t = 2.26$ , d.f. = 21,  $p < 0.05$ ; sit,  $t = 2.33$ , d.f. = 21,  $p < 0.05$ ). During the early and mid nestling stages, 1992 males flew and sat the same as 1991 males (ND 3, fly,  $t = 0.11$ , d.f. = 23,  $p > 0.90$ ; sit,  $t = 0.08$ , d.f. = 23,  $p > 0.90$ ; ND 10, fly,  $t = 1.88$ , d.f. = 20,  $p > 0.07$ ; sit,  $t = 1.86$ , d.f. = 20,  $p > 0.07$ ). During the late nestling period, males in 1992 flew more and sat less than males in 1991 (fly,  $t = 3.51$ , d.f. = 20,  $p < 0.002$ ; sit,  $t = 3.41$ , d.f. = 20,  $p < 0.002$ ). Thus, males in 1992 flew more and sat less than males in 1991 only during the late incubation and the late nestling periods. Thus, males in 1992 worked harder only at the end of the incubation and nestling stages.

## THE FOOD SUPPLEMENTATION EXPERIMENT

### Life History Traits

#### First Broods

Pairs used in the experiment had the same mean first egg dates (control,  $132.7 \pm 0.3$  days, May 11,  $n = 21$ ; supplemented,  $133.3 \pm 0.3$  days, May 12,  $n = 19$ ;  $t = 0.15$ , d.f. = 38,  $p > 0.80$ ) and thus began the nesting cycle at the same time. However, mean clutch size for supplemented nests was larger than for control nests (control,  $5.5 \pm 0.1$  eggs,  $n$



= 25; supplemented,  $5.9 \pm 0.1$  eggs,  $n = 19$ ;  $t = 3.32$ , d.f. = 40.5,  $p < 0.002$ ). This was because of constraints of sample size and the need to use certain boxes for other experiments. To account for the variation in clutch size, clutch size was placed into the ANCOVA models when necessary. Supplemented and control pairs had the same mean incubation length (control,  $15.3 \pm 0.3$  days,  $n = 21$ ; supplemented,  $14.5 \pm 0.3$  days,  $n = 19$ ;  $t = 1.76$ , d.f. = 38,  $p > 0.08$ ) and hatch dates (control,  $154.4 \pm 0.2$  days, June 2,  $n = 25$ , supplemented,  $151.7 \pm 0.3$  days, May 30,  $n = 19$ ;  $t = 0.68$ , d.f. = 42,  $p > 0.40$ ). Regardless of the difference in clutch size, supplemented and control nests had the same mean brood size on ND 6 (controls,  $4.9 \pm 0.2$  young,  $n = 25$ ; supplemented,  $5.0 \pm 0.2$  young,  $n = 19$ ;  $t = 0.24$ , d.f. = 42,  $p > 0.80$ ).

## Second Broods

Eight out of 25 (32 %) control pairs attempted second nests while only three out of 19 (16 %) supplemented pairs attempted second nests. This difference was not significant ( $X^2 = 0.77$ , d.f. = 1,  $p > 0.35$ ). Supplemented and control pairs had the same mean interbrood interval from the fledging of young from the first attempt to the laying of eggs in the second attempt (control,  $11.5 \pm 0.2$  days,  $n = 6$ ; supplemented,  $8.3 \pm 0.1$  days,  $n = 3$ ;  $t = 1.04$ , d.f. = 7,  $p > 0.30$ ). Supplemented and control pairs also had the same mean clutch size for the second attempt (control,  $4.6 \pm 0.3$  eggs,  $n = 8$ ; supplemented,  $5.0 \pm 0.6$  eggs,  $n = 3$ ;  $t = 0.59$ , d.f. = 9,  $p > 0.55$ ). Only two of the supplemented pairs successfully raised second brood young to fledging. Control pairs fledged more young, relative to the number of eggs laid, than supplemented pairs did (control pairs fledged 94 % of the eggs laid,  $n = 32$  eggs; supplemented pairs, 60 %,  $n = 15$  eggs;  $X^2 = 6.02$ , d.f. = 1,  $p < 0.02$ ). Body mass comparisons between supplemented and control pairs with second nests were not made because of the small sample size involved.

### Adult females

Females chosen for supplementation began incubation with a mean mass of  $33.6 \pm 0.9$  g ( $n = 5$ ) while control females weighed  $33.8 \pm 0.5$  g ( $n = 15$ ;  $t = 0.22$ , d.f. = 18,  $p > 0.80$ ). There was no difference in the pattern of mass loss between supplemented and control females during the nestling period (Table 7). Throughout the nesting cycle, supplemented females with five-egg clutches lost an average of 0.24 g per day ( $t = 6.24$ ,  $p < 0.001$ ), while supplemented females with six eggs lost 0.18 g per day ( $t = 16.38$ ,  $p < 0.001$ ; Fig. 13). Control females with five-egg clutches lost 0.12 g per day ( $t = 11.59$ ,  $p < 0.001$ ) and control females with six eggs lost 0.14 g per day ( $t = 13.03$ ,  $p < 0.001$ ). While there was no effect of treatment or clutch size on female mass, supplemented females lost mass at a faster rate than did control females (exp\*day,  $F = 17.12$ , d.f. = 1, 614,  $p < 0.001$ ; all other factors,  $F \leq 3.04$ , d.f.  $\geq 1$ , 43.86,  $p > 0.08$ ). This was true for both clutch sizes because supplemented females consistently lost mass at a faster rate than control females (CS 5:  $t = 2.90$ ,  $p < 0.005$ ; CS 6:  $t = 2.64$ ,  $p < 0.01$ ).

When the nesting cycle was separated into incubation and the nestling stage, supplemented females with five-egg clutches maintained mass during incubation ( $t = 0.28$ ,  $p > 0.75$ ) while supplemented females with six eggs lost an average of 0.12 g per day ( $t = 2.47$ ,  $p < 0.02$ ). Control females with five-egg clutches lost 0.18 g per day ( $t = 5.21$ ,  $p < 0.001$ ), and control females with six eggs maintained mass ( $t = 0.11$ ,  $p > 0.90$ ). Nonetheless, treatment and clutch size had no effect on female mass, and females lost mass at the same rate regardless of treatment. However, clutch size had a significant effect on the rate of mass change (clutch\*day,  $F = 9.65$ , d.f. = 1, 204,  $p < 0.005$ ; all other factors,  $F \leq 3.66$ , d.f.  $\geq 1$ , 36.94,  $p > 0.05$ ). While supplemented females with different clutch sizes lost mass at the same rate ( $t = 0.94$ ,  $p > 0.30$ ), control females with five eggs lost mass at a faster rate than did control females with six eggs ( $t = 3.54$ ,  $p < 0.001$ ). However, supplemented and control females lost mass at the same rate, regardless of clutch size.

Table 7. Comparison of the patterns of mass loss between supplemented and control females during the nestling period using a Mixed-model Analysis of Covariance (ANCOVA). Individual bird is a random variable, and day is the day within the nestling period.

| VARIABLE           | F VALUE    | DEGREES OF FREEDOM | P         |
|--------------------|------------|--------------------|-----------|
| Experiment         | F = 1.78   | d.f. = 1, 80.32    | p > 0.15  |
| Bird(Experiment)   | F = 17.83  | d.f. = 45, 379     | p < 0.001 |
| Day                | F = 143.68 | d.f. = 1, 379      | p < 0.001 |
| Day*Experiment     | F = 0.89   | d.f. = 1, 379      | p > 0.30  |
| Day*Day            | F = 40.49  | d.f. = 1, 379      | p < 0.001 |
| Day*Day*Experiment | F = 1.04   | d.f. = 1, 379      | p > 0.30  |

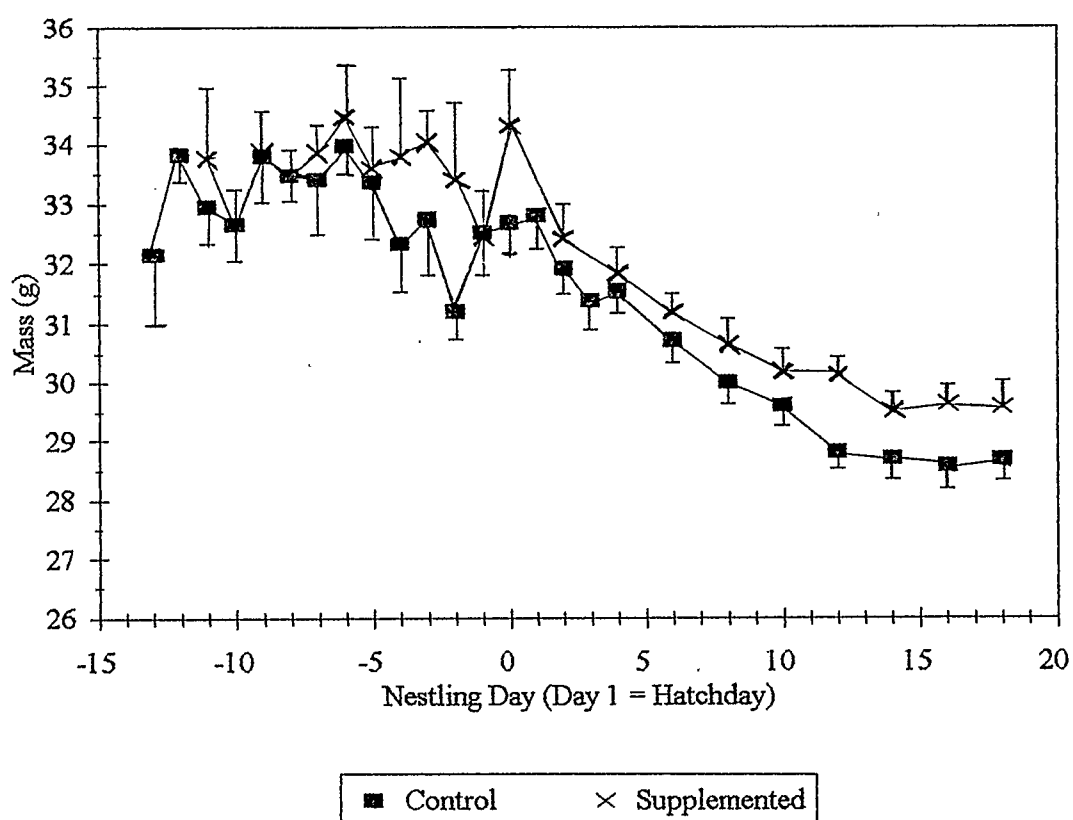


Fig. 13. Mass variation patterns in mean mass ( $\pm$  SE) per nestling day for supplemented and control females during the first brood attempt in 1992. Sample size ranged from 5 to 14 individuals during incubation and from 11 to 28 individuals during the nestling period.

During the nestling stage, supplemented females with five-egg clutches lost an average of 0.33 g per day ( $t = 5.83$ ,  $p < 0.001$ ) while supplemented females with six eggs lost 0.19 g per day ( $t = 11.31$ ,  $p < 0.001$ ). Control females with five eggs lost 0.20 g per day ( $t = 11.46$ ,  $p < 0.001$ ), and control females with six eggs lost 0.25 g per day ( $t = 13.39$ ,  $p < 0.001$ ). Treatment and clutch size had no effect on female mass or the rate of mass change. However, there was a significant three-way interaction of treatment, clutch, and day ( $\text{exp} \times \text{clutch} \times \text{day}$ ,  $F = 8.57$ ,  $\text{d.f.} = 1, 355$ ,  $p < 0.005$ ; all other factors,  $F \leq 1.90$ ,  $\text{d.f.} \geq 1$ ,  $59.11$ ,  $p > 0.15$ ). The slopes were then compared using a corrected significance level of 0.0127. Although not statistically significant, supplemented females with five eggs lost mass at a faster rate than did supplemented females with six eggs ( $t = 2.35$ ,  $p > 0.015$ ), and control females with six eggs lost mass at a faster rate than control females with five eggs ( $t = 1.95$ ,  $p > 0.05$ ). Similarly, supplemented females with five eggs lost mass faster than did control females with five eggs ( $t = 2.19$ ,  $p > 0.02$ ), whereas control females with six eggs lost mass at a faster rate than supplemented females with six eggs ( $t = 2.32$ ,  $p > 0.02$ ). These differences, although not significant, made the three-way interaction significant. At the end of the nestling stage, supplemented females had a mean mass of  $29.6 \pm 0.4$  g ( $n = 16$ ) whereas control females weighed  $28.7 \pm 0.4$  g ( $n = 22$ ), and there was no difference in female mass at this time ( $t = 1.70$ ,  $\text{d.f.} = 36$ ,  $p > 0.09$ ).

During the early nestling phase, supplemented females with five-egg clutches lost an average of 0.47 g per day ( $t = 2.19$ ,  $p < 0.05$ ), whereas supplemented females with six eggs lost 0.33 g per day ( $t = 3.80$ ,  $p < 0.001$ ). Control females with five-egg clutches lost 0.20 g ( $t = 2.21$ ,  $p < 0.05$ ), whereas control females with six eggs lost 0.40 g per day ( $t = 4.34$ ,  $p < 0.001$ ). There was no effect of treatment or clutch size on female mass, and females lost mass at the same rate regardless of treatment or clutch size (all factors,  $F \leq 1.66$ ,  $\text{d.f.} \geq 1$ ,  $43.79$ ,  $p > 0.15$ ). Thus, although a great deal of mass was lost during

the early nestling phase, supplemented and control females had the same mass and lost mass at the same rate.

During the mid nestling phase, supplemented females maintained mass regardless of clutch size (CS 5,  $t = 1.00$ ,  $p > 0.30$ ; CS 6,  $t = 1.23$ ,  $p > 0.20$ ). Control females with five-egg clutches lost an average of 0.32 g per day ( $t = 3.98$ ,  $p < 0.01$ ), whereas control females with six eggs lost 0.28 g per day ( $t = 3.31$ ,  $p < 0.005$ ). Again, there was no statistical effect of treatment or clutch size on female mass, and female mass changed at the same rate regardless of treatment or clutch size (all factors,  $F \leq 3.37$ , d.f.  $\geq 1$ , 39.07,  $p > 0.07$ ).

During the late nestling phase, females with both clutch sizes from both treatments maintained mass ( $t \leq 1.08$ ,  $p \geq 0.25$ , in every case). There was no effect of treatment or clutch size on female mass, and mass varied at the same rate regardless of treatment. However, there was a slight effect of clutch size by treatment (clutch\*exp,  $F = 4.54$ , d.f. = 1, 35.63,  $p < 0.05$ ; all other factors,  $F \leq 0.85$ , d.f.  $\geq 1$ , 35.73,  $p > 0.35$ ). Thus, the difference in mass between supplemented and control females with five eggs was different from the difference in mass between the treatment groups with six-egg clutches. Females maintained mass during the late nestling phase, and there was no difference in the rate of mass change between supplemented and control females. Thus at all three nestling phases, supplemented and control females with both clutch sizes lost mass at the same rates, and the mass loss occurred in the early and mid nestling stages. However, control females consistently, although not significantly, lost mass at a faster rate than supplemented females did.

In summary, supplemented females lost mass at a faster rate than did control females when the entire nesting cycle was analyzed. Supplemented and control females began incubation at the same mass. During incubation, while supplemented females lost mass and control females maintained mass, the rate of mass change between the two treatments was not statistically different. Clutch size was a significant factor during the

nestling stage. Supplemented females with five eggs lost mass at a faster rate than did supplemented females with six eggs, and control females with six eggs lost mass faster than did control females with five eggs. In females with five-egg clutches, supplemented females lost mass at a faster rate than did control females. For females with six-egg clutches, control females lost mass at a faster rate than did supplemented females. During the three nestling phases, treatment had no effect on female mass or the rate of mass loss, and most of the mass loss occurred in the first half of the nestling stage. From the beginning of incubation through to the end of the nestling stage, supplemented females lost 4.2 g in total, or 12 % of their initial body mass. Control females lost 4.2 g in total, or 13 % of their mass.

### **Adult Males**

Supplemented males began the incubation period at a mean mass of  $30.0 \pm 0.4$  g ( $n = 10$ ), while control males weighed  $30.5 \pm 0.4$  g ( $n = 11$ ;  $t = 0.78$ , d.f. = 19,  $p > 0.40$ ). While supplemented males with five-egg clutches maintained mass ( $t = 1.37$ ,  $p > 0.15$ ), supplemented males with six eggs lost an average of 0.02 g per day during the nesting cycle ( $t = 2.66$ ,  $p < 0.01$ ). Control males with five-egg clutches lost 0.05 g per day ( $t = 6.83$ ,  $p < 0.001$ ) whereas control males with six eggs lost 0.03 g per day ( $t = 2.62$ ,  $p < 0.01$ ; Fig. 14). Treatment and clutch size had no effect on male mass, and males with different clutch sizes lost mass at the same rate. However, there were significant effects of treatment by day and treatment by clutch by day on mass (exp\*day,  $F = 11.23$ , d.f. = 1, 515,  $p < 0.001$ ; exp\*clutch\*day,  $F = 7.72$ , d.f. = 1, 515,  $p < 0.01$ ; all other factors,  $F \leq 0.70$ , d.f.  $\geq 1$ , 44.24,  $p > 0.40$ ). The slopes were then compared using the corrected significance level of 0.0127. Control males with five eggs lost mass faster than did supplemented males with five eggs ( $t = 3.37$ ,  $p < 0.001$ ). Males with six eggs lost mass at the same rate regardless of treatment ( $t = 0.69$ ,  $p > 0.45$ ). In addition, although not

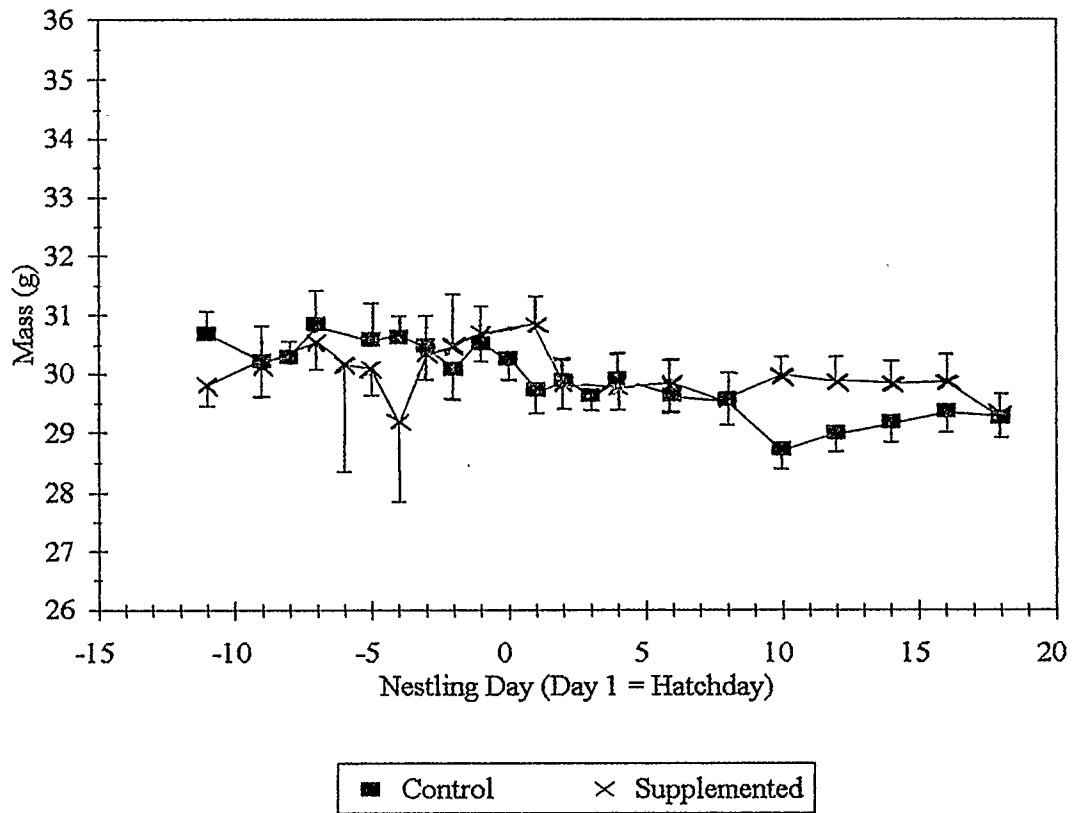


Fig. 14. Mass variation patterns in mean mass ( $\pm$  SE) per nestling day for supplemented and control males during the first brood attempt in 1992. Sample size ranged from 5 to 14 individuals during incubation and from 11 to 28 individuals during the nestling period.



significant, control males with five eggs lost mass faster than did control males with six-egg clutches ( $t = 2.20$ ,  $p > 0.02$ ). This explains the significant three-way interaction.

When the nesting cycle was separated into incubation and the nestling stage, supplemented males with five-egg clutches maintained mass during the incubation period ( $t = 1.53$ ,  $p > 0.10$ ), whereas supplemented males with six eggs gained an average of 0.07 g per day ( $t = 2.63$ ,  $p < 0.01$ ). Control males with five-egg clutches maintained mass ( $t = 0.74$ ,  $p > 0.45$ ) whereas control males with six eggs gained 0.09 g per day ( $t = 2.35$ ,  $p < 0.02$ ). There was no effect of treatment or clutch size on male mass, and male mass varied at the same rates regardless of treatment or clutch size (all factors,  $F \leq 2.80$ , d.f.  $\geq 1$ , 51.17,  $p > 0.09$ ).

During the nestling stage, supplemented males with five-egg clutches gained an average of 0.10 g per day ( $t = 2.60$ ,  $p < 0.01$ ) whereas supplemented males with six eggs lost 0.05 g per day ( $t = 4.06$ ,  $p < 0.001$ ). Control males with five-egg clutches lost 0.07 g per day ( $t = 5.12$ ,  $p < 0.001$ ), and control males with six eggs lost 0.04 g per day ( $t = 2.72$ ,  $p < 0.01$ ). There was no effect of treatment or clutch size on male mass during the nestling stage. However, there were significant effects of treatment and clutch size on the rate of mass change, and there was a significant three-way interaction between treatment, clutch, and day (exp\*day,  $F = 13.63$ , d.f. = 1, 310,  $p < 0.001$ ; clutch\*day,  $F = 6.90$ , d.f. = 1, 310,  $p < 0.01$ ; exp\*clutch\*day,  $F = 14.58$ , d.f. = 1, 310,  $p < 0.001$ ; all other factors,  $F \leq 1.62$ , d.f.  $\geq 1$ , 51.51,  $p > 0.20$ ). Again the slopes were compared using the corrected significance level of 0.0127. Supplemented males with six eggs lost mass at a faster rate than did supplemented males with five eggs ( $t = 3.63$ ,  $p < 0.001$ ). Control males lost mass at the same rate regardless of clutch size ( $t = 1.30$ ,  $p > 0.15$ ). Control males with five-egg clutches lost mass at a faster rate than supplemented males with five eggs ( $t = 4.15$ ,  $p < 0.001$ ), whereas there was no difference in the rate of mass loss between supplemented and control males with six eggs ( $t = 0.15$ ,  $p > 0.85$ ). This explains the significant three way interaction. At the end of the nestling period, supplemented males

had a mean mass of  $29.5 \pm 0.4$  g ( $n = 16$ ), and control males weighed  $29.3 \pm 0.3$  g ( $n = 17$ ). There was no difference in mass between the treatments ( $t = 0.50$ , d.f. = 31,  $p > 0.60$ ).

When the early nestling phase was examined, supplemented males with five-egg clutches lost an average of 0.34 g per day ( $t = 2.67$ ,  $p < 0.01$ ), whereas supplemented males with six eggs maintained mass ( $t = 1.04$ ,  $p > 0.30$ ). Control males with five eggs lost 0.18 g per day ( $t = 2.95$ ,  $p < 0.005$ ), whereas control males with six eggs maintained mass ( $t = 0.31$ ,  $p > 0.75$ ). There was no effect of treatment or clutch size on male mass. Although there was no effect of treatment on the rate of mass change, there was an effect of clutch size (clutch\*day,  $F = 8.94$ , d.f. = 1, 104,  $p < 0.005$ ; all other factors,  $F \leq 1.75$ , d.f.  $\geq 1$ , 38.71,  $p > 0.15$ ). Although not significant, supplemented males with five-egg clutches lost mass faster than did supplemented males with six eggs ( $t = 2.11$ ,  $p > 0.03$ ). The same was true for control males as well ( $t = 2.17$ ,  $p > 0.03$ ). Thus, males with different clutch sizes lost mass at different rates in both treatments.

During the mid nestling phase, males maintained mass regardless of treatment and clutch size ( $t \leq 1.57$ ,  $p \geq 0.10$  in every case). There was no effect of treatment or clutch size on male mass. However, there was an effect of treatment on the rate of mass change (exp\*day,  $F = 4.24$ , d.f. = 1, 64,  $p < 0.05$ ; all other factors,  $F < 1.96$ , d.f.  $> 1$ , 35.80,  $p > 0.15$ ). Supplemented and control males lost mass at the same rate regardless of clutch size (CS 5:  $t = 1.53$ ,  $p > 0.10$ ; CS 6:  $t = 1.68$ ,  $p > 0.09$ ). Although not significant, control males lost mass at a slightly faster rate than supplemented males at both clutch sizes.

Males maintained mass during the late nestling phase, regardless of treatment or clutch size ( $t \leq 1.50$ ,  $p > 0.10$  in every case), and treatment and clutch size did not affect mass or the rate of mass change (all factors,  $F \leq 1.89$ , d.f.  $\geq 1$ , 33.61,  $p > 0.15$ ). Thus, supplemented and control males had the same mass and mass varied at the same rate during the late nestling phase.

Supplemented males had similar body-mass dynamics compared to control males. Supplemented and control males began incubation at the same mass. Both supplemented and control males maintained or gained mass during incubation, and both treatments lost mass during the nestling period. However, clutch size was again important during the nestling stage, and control males with five-egg clutches lost mass faster than supplemented males with five eggs. Males with six-egg clutches lost mass at the same rates regardless of treatment. Males in both treatments had the same mass and lost mass at the same rates in the three nestling phases, except for the mid nestling phase where control males lost mass at a faster rate. From the beginning of incubation through to the end of the nestling period, supplemented males lost 0.8 g in total, or close to 3 % of their initial body mass. Control males lost 1.4 g in total, or close to 5 % of their body mass.

### **Nestlings**

On ND 6, there was no difference in mass or tarsus length between supplemented and control nestlings (mass,  $t = 0.77$ , d.f. = 187.9,  $p > 0.40$ ; tarsus,  $t = 0.26$ , d.f. = 181.6,  $p > 0.75$ ). There was no difference between supplemented and control nestlings in mass on ND 12, but supplemented nestlings had longer tarsi (mass,  $t = 0.36$ , d.f. = 176.3,  $p > 0.70$ ; tarsus,  $t = 2.50$ , d.f. = 184,  $p < 0.02$ ). There was no difference in either mass or tarsus length on ND 18 (mass,  $t = 1.92$ , d.f. = 154.8,  $p > 0.05$ ; tarsus,  $t = 1.02$ , d.f. = 84,  $p > 0.30$ ). Thus, the only difference between supplemented and control nestlings occurred on ND 12 with tarsus length.

There were 92 nestlings in 19 supplemented nests and 123 nestlings in 25 control nests. While 11 nestlings (9 %) from four control nest boxes died due to starvation or hypothermia, only one (1 %) supplemented nestling died (cause of death unknown). Nine of the 11 control nestlings died during a snow-storm with sub-freezing temperatures in mid-May. Most of the control adults with nestlings deserted their young during the

storm, and the nestlings died of starvation and/or hypothermia. While only one control nest with nestlings survived the storm, all of the supplemented young survived.

## **DISCUSSION**

### **Unfavourable Conditions in 1992**

Environmental conditions early in the nesting cycle are critical to Mountain Bluebird reproductive success because eggs and small nestlings are especially sensitive to the thermal environment (Marsh 1980; Houston 1982; Mertens 1987; Webb 1987). Environmental conditions in May are especially important because Mountain Bluebirds lay eggs and incubate clutches in early May, and hatching begins in mid-May. Overall, 1992 appeared to be a much less favourable year than 1991 was, especially during the month of May. Although not significant, temperatures were cooler and there were more days with rain in May 1992 than in May 1991. In addition, although there were storms in both years, the storm in 1992 was more severe, with sub-freezing temperatures and snow which lasted on the ground for several days. Females lost an average of two and a half grams during the storm and never regained that lost mass. Thus, females did not seem to be able to maintain adequate body fat reserves, and they temporarily abandoned their clutches, prolonging the incubation period. Nestlings that hatched prior to the storm were either abandoned or had slower growth than did nestlings hatched after the storm. In addition, workload was greater for parents in 1992 as demonstrated by the observation that both males and females spent more time in flight during the second half of the nestling phase in 1992 than in 1991. Also, nestlings in 1992 grew slower than did nestlings in 1991. Thus, the combination of cool temperatures, precipitation, and a severe snow storm during a critical period in the nesting cycle led to reduced Mountain

Bluebird productivity, increased workload for the adults, and slower nestling growth in 1992 as compared to 1991 (Pearman 1991, 1992).

### **Patterns of Variation in Adult Body Mass**

In Mountain Bluebirds, males and females have very different patterns of body mass variation during the reproductive cycle. Prior to egg laying, females gained mass whereas males did not. Because Mountain Bluebird males and females are nearly identical in size (males are actually slightly larger; Power 1980), females were heavier than males for their size. Females may need this extra mass for egg laying, incubating, and brooding purposes. Body fat reserves may allow incubating or brooding females to maintain nest attentiveness during periods of poor foraging conditions (Newton et al. 1983; Ekman and Hake 1990). Extra body fat reserves would also allow the female to minimize foraging time and increase incubation and brooding time (Sherry et al. 1980). Canada geese (*Branta canadensis*), for example, have high nest attentiveness and derive 87 % of their energy requirements from body reserves during incubation (Murphy and Boag 1989). Indeed, food supply may limit the start of breeding because females may not lay eggs until they have gained sufficient body fat reserves for incubating and brooding purposes (Bryant 1979; Drent and Daan 1980).

While females accumulated extra body fat reserves for the first breeding attempt, males maintained a low body mass. As in many passerines, male Mountain Bluebirds do not have brood patches and do not incubate or brood. Since males are thus not constrained to the nest, they have more time available for self maintenance and, presumably, do not require as extensive an energy reserve. Males should also benefit from maintaining a low body mass because this reduces flight costs and increases flight performance by increasing maneuverability, flight speed, and acceleration (Andersson and Norberg 1981). Increased flight performance would allow males to attack

conspecifics more efficiently or to avoid predation (Lima 1986) or provide more time to seek extra-pair copulations from neighbouring females.

At the beginning of the incubation period, female Mountain Bluebirds were heavier than males, and females in 1991 were heavier than females in 1992, the latter presumably because of more favourable spring conditions in 1991 (see also Ekman and Hake 1990; Hurly 1992). In both years, females began losing fat reserves during incubation, although the patterns of mass loss were not the same. Females in 1991 lost mass only near the end of the incubation period, just prior to hatching, whereas females in 1992 lost some mass over the entire incubation period.

Energy reserves may be particularly important to Mountain Bluebird females, especially during incubation. Females must spend most of their time on the nest, thus reducing the time available for foraging (Jones 1987b; Williams 1993). At the same time, however, energy expenditure can be high and foraging success unpredictable. Females must produce heat above normal thermoregulatory costs, and they must rewarm cool eggs. Ambient temperatures are often low at the time of incubation, and food levels may be reduced (Williams 1993). Indeed, May temperatures in both years, but especially in 1992, were lower than temperatures later in the breeding season. In addition, in 1992 there were more days with rain in May than in months later in the breeding season. Extra resources in the form of body fat reserves may aid the female through stressful periods of cool temperatures and increased precipitation (Drent and Daan 1980; Meijer et al. 1989), thus allowing the female increased time for nest attentiveness. Extra body fat reserves may thus serve as insurance against poor foraging conditions, and this benefit presumably outweighs the costs of additional mass in terms of decreased flight efficiency and performance. The benefits of the fat reserves were evident in the rapid mass loss during the spring storms. It is likely that, without the reserves, more females would have had to abandon their nests because they could not meet the energy requirements of incubating eggs or brooding young. Overall, females in 1992 were forced to tap into

their body fat reserves during incubation while conditions were generally more favourable in 1991, and females maintained their mass.

Energy reserves may be especially important for the Mountain Bluebird, because it is an early breeder and is likely to encounter unpredictable foraging conditions. I would predict that species that breed later in the season would have smaller energy reserves because conditions are more favourable at this time. Unfortunately, body mass data are scarce, and the patterns of mass variation for late-breeding species are not known.

Male Mountain Bluebirds maintained a low body mass during the incubation stage in both years, presumably because males do not incubate and thus extra energy reserves are not as crucial. Because males are not constrained to the nest for incubating or brooding purposes and they have more time available for self maintenance, the benefits of extra energy reserves are lower than for females. Therefore, males do not put on extra mass. It might be predicted that in species in which both sexes incubate, males would put on body fat reserves in a pattern similar to that of females. In European Starlings, in which both sexes do incubate, males are heavy during incubation and then lose mass during the nestling period, although sample sizes for males are small (Ricklefs and Hussell 1984). In Bank Swallows and Swallows, in which the male may incubate, male body mass increases during incubation, and decreases during the nestling period. However, males are lighter than females at all stages of the nesting cycle (Petersen 1955; Jones 1987d). This may be because males are not constrained by egg laying and do not require extra energy reserves for that function, or because the female is the principal incubator. At any rate, incubating birds gain mass because the benefits of increased mass for incubating birds seem to outweigh the costs of carrying that extra mass. Birds that are not constrained by incubation and brooding do not carry extra body fat reserves. The optimal mass for non-incubating birds, such as male Mountain Bluebirds during the incubation period, is thus lower than the optimal mass for incubating birds. In addition,

low body mass would make it easier for the non-incubating bird to defend the territory, protect the incubator and the eggs or young, and perhaps seek extra pair copulations.

The hatching period may be a critical time in the nesting cycle because young must be fed in addition to being kept warm. Both sexes lost mass during the hatching period in 1991, with females losing mass at a faster rate than did males. Both sexes maintained mass during the hatching period in 1992. The hatch period may be a stressful time for both parents because of the burden of feeding newly-hatched young. Male Mountain Bluebirds help feed at all nestling stages, but only the female broods. Thus, the female must allocate time to brooding, feeding altricial young, and self maintenance. Energy reserves may again be used to reduce foraging time, thereby allowing more time for brooding. However, the young require small prey items which must be brought back to the nest, and foraging for these items restricts the time available for brooding and self-maintenance (Freed 1981; Martin 1987). Jones (1987d), however, did not find that female mass loss during brooding was a consequence of limited time for self feeding. Indeed, adults may have ample time to feed themselves while they forage for their young (Jones 1987e).

Energy demands on the parents are at a peak during the nestling stage (Bryant and Westerterp 1983; Martin 1987; Moreno and Hilstrom 1992), and nestlings grow rapidly and require a great deal of food (Mock et al. 1991). Males in 1991 maintained mass during the nestling period, while females in both years, and males in 1992, lost mass at this time. Again, females had greater mass loss than males did. Thus, the overall pattern of mass variation in females was an increase in mass prior to egg laying and incubation, with mass loss beginning during the incubation period, and then continued loss of mass into the hatching and nestling periods. Males maintained a constant mass throughout the entire nesting cycle unless conditions became unfavourable, in which case males lost some mass.



### Mass Variation Patterns in Other Species

Patterns of body mass variation similar to that found in Mountain Bluebirds occur in other species as well. As in my study, female Bank Swallows (Petersen 1955), House Wrens (Freed 1981), Pied Flycatchers (Silverin 1981), Yellow-rumped Caciques (Cacicus cela; Robinson 1986), Swallows (Jones 1987d), Wood Thrushes (Hylocichla mustelina, Johnson et al. 1990), Collared Flycatchers (Ficedula albicollis; Moreno et al. 1991) and Green-rumped Parrotlets (Forpus passerinus, Curlee and Beissinger, in review) are significantly heavier than males from the start of egg laying through hatching and the beginning of the nestling period. At the end of the nestling period, females of these species have the same mass or a slightly lower mass than do males. In contrast, in Northern Orioles (Icterus galbula, Biermann and Sealy 1985), Yellow Warblers (Dendroica petechia, Biermann and Sealy 1985), and Red-throated Bee-eaters (Merops bullocki, Crick and Fry 1986), females are heavier than males only during egg laying, while in Eastern Kingbirds (Tyrannus tyrannus), there is no difference between male and female mass at any stage (Biermann and Sealy 1985). Unfortunately, Biermann and Sealy (1985) were not able to follow mass variation patterns of individuals, and thus, the exact timing and the specifics of mass changes are not known. In addition, late breeders or birds that do not encounter seasonally-unpredictable foraging conditions should not require extra body fat reserves. In these species females and males should have the same body mass.

### Workload During the Nestling Phase

The nestling period may be an especially critical time in the Mountain Bluebird nesting cycle because energetic demands are greater at this time than at any of the other nesting stages (Bryant and Westerterp 1983). In both years, male and female Mountain Bluebirds spent more time in flight during the nestling period than during the incubation stage. Sullivan (1990) also found that parents feeding young spent more time in flight

than incubating parents did. Mountain Bluebird nestlings grew the fastest during the mid nestling phase (see also Mock et al. 1991), and the energetic needs of nestlings increase rapidly (Ricklefs 1974; Mock et al. 1991). Energetic demands on the parents are thus high at this time (Bryant and Westerterp 1983; Moreno and Hilstrom 1992), and feeding rate increases with nestling age (Carey 1990; Yasukawa et al. 1990; Conrad and Robertson 1993). By the late nestling phase the young have obtained adult mass and require the most energy (Ricklefs 1974; Mock et al. 1991). Thus, the mid and late nestling phases are likely the most demanding period of the breeding cycle. This is supported by the fact that in the morning adult Mountain Bluebirds in 1992 spent more time flying during the second half of the nestling stage than the first half. Adults also had the highest feeding rates during the mid and late nestling stages, especially in the morning. Feeding rate in the morning may be especially critical because the adults and young have fasted all night. In addition, although I could not measure load size and prey size, both may increase with nestling age (Jones 1987d,e; Moreno 1987). Workload may increase more than feeding rate suggests. Thus, the second half of the nestling period appears to be the most demanding period of the Mountain Bluebird nesting cycle.

Not all of my results support the idea that workload is greatest during the mid or late nestling phases. Although Mountain Bluebirds in 1991 did increase their time in flight for the nestling period, in the early evening both sexes flew the most during the early nestling phase. The young require small food items, such as spiders and small larvae (Cummings 1986; Moreno and Hilstrom 1992), which may be difficult to find. Thus, parents may have to spend more time searching for small food items. Also, the young may require many feeding trips, although each trip involves just a small food item. Females may also need to return to the nest to brood, especially if temperatures are low (Marsh 1980). Although this evidence supports the idea that the first half of the nestling period is energetically demanding, the workload of the adults during the second half of

the nestling period in 1991 may have been underestimated because data were not collected in the mornings and feeding data were not collected at all.

## **Testing the Hypotheses**

### **Adult Body Mass Variation Patterns**

According to Norberg's (1981) flight adaptation hypothesis, body mass loss should occur prior to the period of greatest energetic demand on the parents (i.e., prior to the mid or late nestling phases). I also predicted that mass loss should follow a decelerating pattern during the nestling period. According to the stress hypothesis, mass loss should occur as the nestlings grow, with the most loss at the time of maximum nestling demand (i.e., the mid or late nestling phases). Thus, mass loss by adults rearing young would follow an accelerating pattern if the stress of caring for the young was a factor. My data support the flight adaptation hypothesis. Female Mountain Bluebirds in 1991 maintained mass during incubation, and significant rapid mass loss began during the hatching period and continued into the nestling period. Mass loss occurred prior to the mid nestling period, and in females, mass loss followed a decelerating pattern. This strongly supports the flight adaptation hypothesis. Significant mass loss for females in 1992 began during incubation and continued into the early and the mid nestling phases. Again, mass loss in females during the nestling stage followed a decelerating pattern providing further support for the flight adaptation hypothesis.

Since mass loss by Mountain Bluebird males in both years was minimal or nonexistent, little can be said regarding the timing of mass loss in support of either hypothesis. While males in 1991 lost mass during the hatching period, males in 1992 lost mass throughout the nestling period. Loss early in the nestling period would provide additional evidence for the flight adaptation hypothesis, while mass loss later in the nestling stage suggests stress.

Comparing the sexes, once the brooding period was over, males and females spent equal amounts of time in flight, and they fed the nestlings at equal rates. According to the flight adaptation hypothesis, with both sexes being of similar size and having equal work load, both sexes should have the same body mass since the costs and benefits of fat reserves should be the same for both sexes. Thus, it might be expected that females would lose more mass than males because they were heavier during egg laying and incubation. This would allow females to reach the same low body mass as males. According to the stress hypothesis, because males and females were working at equal rates, mass loss would be the same for both sexes, and females should have a greater mass at the end of the nesting cycle. In both years, females lost more mass than did males during the nestling period, and females had the same low mass as males by the end of the nesting cycle. This strongly supports the flight adaptation hypothesis.

#### Mass Variation Patterns During the Second Brood Attempt

Since there appears to be a benefit to increased mass for laying and incubation, the flight adaptation hypothesis led to the prediction that females attempting a second brood would regain some of the lost mass prior to egg laying and then lose mass in a pattern similar to that in the first brood attempt, achieving the same low body mass. Females would not necessarily have to reach the same level of body fat reserves as they had in the first attempt because conditions are more favourable and more predictable during the second attempt and females could afford smaller energy reserves. According to the stress hypothesis, females would regain mass for the second brood and would lose mass if stress was again a factor. The amount of mass loss would vary depending on the stress. Females appear to use the interbrood interval to regain mass for the second attempt, and the amount of available food may regulate the length of this interval (Drent and Daan 1980). In 1991, females were about 1.5 g lighter at the beginning of the second brood attempt than they were at the beginning of the first brood attempt, and females in

both years lost mass at the same or faster rate in the first attempt as they did in the second. Females also had the same mass at the end of each attempt, even though conditions had changed, supporting the idea that there is an optimal body mass for flight.

### Variation in Adult Body Mass Between Years

According to the flight adaptation hypothesis, in two different years, mass loss patterns should be the same because there is an optimum body mass for flight during the nestling stage. According to the stress hypothesis, greater and faster loss should occur in a colder, wetter year due to poor foraging conditions. Even though 1992 was less favourable than 1991, females in the two years lost mass at the same rate when the entire nesting cycle was considered. This was also true when only the incubation period was considered. Females in both years followed the same pattern of decelerating mass loss during the nestling period. In addition, females had the same mass at the end of the first breeding attempt regardless of year. These results support the flight adaptation hypothesis. Since a stable mass was achieved prior to the peak demand, and the final mass was constant from year to year, I viewed this as strong evidence for the flight adaptation hypothesis. Additional evidence for the flight adaptation hypothesis was provided by the second brood attempt, as females again lost mass at the same rate and had the same mass at the end of the nesting cycle regardless of year.

### Year to Year Variation in Nestling Growth Patterns

Nestlings exhibited sigmoidal growth in both years, with a plateau at approximately adult mass. Growth in altricial nestlings has a maximum rate set by physiological constraints, but this rate can be reduced if daily costs cannot be met by the parents (Ricklefs 1969; Drent and Daan 1980). Control nestlings in 1992 were significantly lighter than nestlings in 1991 at all three nestling stages. In addition, nestlings in 1992 had smaller tarsi on ND 6 and ND 12 than nestlings in 1991 did. Thus,

nestlings in 1992 grew more slowly than their counterparts in 1991. This suggests that adults in 1992 were energetically stressed, as they could not maintain nestling growth rates, and nestlings were lighter at the time of fledging compared to those in 1991. Mass differences at fledging are related to chick quality and subsequent survival in a few species (Perrins 1965; Askenmo 1977; Garnett 1981; and Nur 1984c; but see Tinbergen and Boerlijst 1990). The evidence is scanty, and it is not known whether fledging mass has an effect on Mountain Bluebird nestling survival. In addition, the nestling period may have been prolonged in 1992, allowing nestlings to attain the optimal fledging mass. However, I was not able to determine if this was the case because nestlings were handled on ND 18, and handling nestlings late in the nestling period can cause premature fledging (Scriven 1990).

#### The Food Supplementation Experiment

The main test of the two hypotheses was the food supplementation experiment in which Mountain Bluebird pairs and their young were provided with 25 % of their daily energy needs. According to the flight adaptation hypothesis, supplemented birds should lose mass in a pattern and at a rate similar to that of control birds because there is an optimal body mass for flight. The stress hypothesis predicts that supplemented birds do not lose mass or lose less mass because some of the stress of reproduction is removed. Supplemented females actually lost mass at a faster rate than controls did when the entire nesting cycle was considered, and supplemented females lost mass at the same rate as control females during the incubation stage. Supplemented females followed the same decelerating pattern of mass loss as the control females did. In addition, supplemented and control females had the same low body mass at the end of the nesting cycle. All of these results support the flight adaptation hypothesis. However, control females lost mass at a faster rate than supplemented females did during the nestling stage, especially during the mid nestling phase. This is evidence for the stress hypothesis. Thus,

supplemented and control females follow the same mass variation patterns until the nestling stage. At this time, the nestlings placed great energetic demands on the parents. Because supplemented females were provided with extra energy, they had less difficulty meeting these demands than did control females, who had to tap body fat reserves to meet the needs of their young.

Following the flight adaptation and the stress hypotheses, the same predictions were made for supplemented and control males. Supplemented and control males had the same mass at the end of the nesting cycle which provides additional evidence for the flight adaptation hypothesis because males maintained the same low body mass regardless of treatment. This also provides evidence that males do not require extra body fat reserves during the nesting cycle. Males provided with a supplemental food source had ample opportunity to add body fat reserves, yet they did not. Control males did lose mass at a faster rate than supplemented males did, when the entire nesting cycle or only the nestling period was considered. This supports the stress hypothesis.

#### Nestling Growth Patterns and Time Activity Budgets in Relation to Treatment

Although the rates of mass loss differed between control and supplemented birds, they had the same mass at the end of the nesting cycle. It might thus have been expected that the extra energy obtained from the supplement would have gone into nestling growth, since it was not seen in adult body mass. Supplemented Carrion Crows (Corvus corone) had heavier and larger fledglings than did controls (Richner 1992). However, Mountain Bluebird nestlings had the same mass at each stage, regardless of treatment. Nestling tarsus was the same for both groups at each stage except for ND 12, where supplemented nestlings had slightly longer tarsi. Nestlings had the same mass at the time of fledging, despite the fact that additional mass may increase the survival of young birds (Perrins 1965; Askenmo 1977; Garnett 1981; Nur 1984c).

Supplemented adults could also have used the extra energy to reduce time spent foraging. Arcese (1989) found that supplemented Song Sparrows (*Melospiza melodia*) decreased time spent foraging, increased their body mass, and spent a greater proportion of their time in surveillance. Mountain Bluebirds did not put the extra energy into extra body fat reserves, and thereby kept flight costs low. Nor did they put the extra energy into their young. It is possible that supplemented adults reduced the amount of time spent in foraging flight, thus increasing time available for surveillance, territory defense and defense of the young. Unfortunately, time constraints did not allow me to collect time budget data on supplemented pairs.

According to the flight adaptation hypothesis, supplemented pairs should have the same probability of a second brood, and the same interbrood interval, clutch size, reproductive success, and probability of survival as did control pairs during the second brood attempt. According to the stress hypothesis, supplemented pairs should have a greater probability of a second brood, a shorter interbrood interval, a larger clutch size, greater reproductive success, and greater probability of survival. Most of the data from second brood attempts in the food supplementation experiment support the flight adaptation hypothesis. Control and supplemented pairs were equally likely to initiate a second brood. In addition, supplemented and control pairs had the same interbrood interval, and the same clutch size. However, control pairs fledged more young per egg laid than supplemented pairs did. Thus control pairs actually had greater reproductive success than supplemented pairs in the second brood attempt. Unfortunately, it was impossible to collect data on adult survival rates.

### **Evidence for the Flight Adaptation Hypothesis From Other Studies**

Evidence supporting the flight adaptation hypothesis is found in two other studies. Female Red-throated Bee-eaters with helpers lost mass in the same pattern and had the same low body mass during the nestling stage as did females without helpers



(Crick and Fry 1986). When brood size was experimentally manipulated in Green-rumped Parrotlets, adult females lost the same amount of mass regardless of the number of young in the nest (Curlee and Beissinger, in review). In both of the above examples, parents feeding young achieved a low body mass, which would be beneficial for reasons pertaining to flight. Females arrived at the same mass despite differences in work load, suggesting that low body mass was the optimum, a compromise between flight efficiency and insurance against energy shortfall.

Reproduction may be especially costly in an unfavourable year, such as 1992 in my study area. Thus, it would be instructive to perform the supplementation experiment again in a more favourable year. In addition, it would be helpful to collect time budget data on supplemented birds to determine if they fly less or spend less time foraging than control birds do due to the extra energy supply available to them.

## **Conclusion**

In conclusion, my results most strongly support the hypothesis that the adaptive strategy for female Mountain Bluebirds, and possibly for other passerines, is to gain mass prior to egg laying and incubation, use this extra reserve when necessary to reduce foraging time and thereby maintain incubation attentiveness, and lose mass during the nestling period, prior to the period of maximum nestling demand. The extra mass serves as an energy reserve, allowing females to spend more time incubating and brooding during a time when foraging success is unpredictable and energy demand fluctuates. Once predictably high foraging success occurs, and the insurance body fat reserves are no longer needed, females lose mass to decrease flight costs and increase flight performance while caring for their young. By losing approximately 14 % of their body mass, females save an estimated 20 % of their BMR (basal metabolic rate) over 24 hours. This amount of energy is estimated to be equivalent to that required to raise an additional 0.15 young (Norberg 1981) and clearly could be used to raise larger, higher

quality offspring. As males are not constrained to the nest for incubating and brooding purposes and therefore do not need the extra energy reserves, they maintain a low optimal mass throughout the nesting cycle. Thus, both males and females reach a low body mass prior to the maximum demand of their young, and this mass is adaptive for reasons pertaining to flight.

Not all of my results support the flight adaptation hypothesis. The body mass variation patterns of Mountain Bluebird males in 1992 provide strong evidence for the stress hypothesis. Male Mountain Bluebirds do not carry extra energy reserves for breeding purposes, and they maintain a low body mass throughout the breeding season, most likely for reason pertaining to flight. Thus, mass loss beyond the optimal body mass during critical periods of high energy demand, such as during the mid and late nestling phases, is evidence of stress or a cost of reproduction. Males in both breeding attempts in 1992 were lighter at the end of the nesting cycle than males in 1991, although the differences were not significant. Although mass loss by males in 1992 is evidence of stress, the two hypotheses are not entirely mutually exclusive, and mass loss induced by stress may result in savings in energy expended during flight due to decreased wing loading (Gaston and Jones 1989).

Body mass loss has been documented in females of other flying vertebrates including big brown bats (Eptesicus fuscus) and little brown bats (Myotis lucifugus; Burnett and Kunz 1982) and has been interpreted as a result of reproductive stress. Researchers should exercise caution when assuming that mass loss is an indication of stress or a cost of reproduction in any flying organism. My results suggest that Mountain Bluebirds are neither energy limited nor working maximally during reproduction, and evidence of a cost of reproduction was not seen. Much of the change in body fat reserves appears to be an adaptation to enhance foraging flight during reproduction, not a resulting cost of that reproduction.

Body mass loss during the breeding season has also been seen in non-flying vertebrates, including Adelie Penguins (Pygoscelis adeliae; Johnson and West 1973), Red Deer (Cervus elaphus; Albon et al. 1983), and Northern Elephant Seals (Mirounga angustirostris; Costa et al. 1986; Deutsch et al. 1990). With regard to life history strategies, mass loss should not be used as evidence of the cost of reproduction unless the mass change patterns are well known and understood. Adaptive mass loss may reduce the workload of the parents and promote increased survivorship and future fecundity, as well as current reproductive success. This is true for flying as well as non-flying individuals. It may not represent a cost of reproduction or a decrease in condition, and thus a decrease in survival or future fecundity, unless conditions are extremely unfavourable. In addition, researchers should examine the costs and benefits of obtaining extra body fat reserves in the first place. Body fat reserves may serve as insurance against unpredictable foraging conditions. When foraging conditions are more predictable, the extra body fat reserves are lost for reasons pertaining to locomotion

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