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The Nesting Ecology of the Townsend's Solitaire (Myadestes townsendi)

by

Nathaniel Shambaugh

Bachelor of Arts, University of New Hampshire 1979.


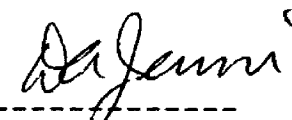
Presented in Partial Fulfillment of the Requirements for the Degree of

Master of Arts

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1987

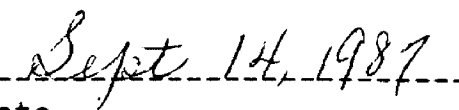
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Zoology

The Nesting Ecology of the Townsend's Solitaire
(Myadestes townsendi). (105pp)

Co-directors: Richard L. Hutto, and Donald A. Jenni.

A two year study was conducted on the nesting ecology of the Townsend's Solitaire (Myadestes townsendi) in Missoula Co., Montana. The Townsend's Solitaire is a ground-nesting thrush that nests on cutbanks associated with streams or dirt roads. Nests were most often found on north-facing cutbanks where there was an overhang of at least 15 cm. The female of a pair built the nest and incubated the eggs without help from the male. Clutch size was generally four, with one egg being laid per day until the clutch was complete. The eggs within a clutch tended to increase in volume from first to last egg laid. Incubation started after the last egg was laid and lasted 12-13 days.

Upon hatching, the altricial young weighed approximately 7% of adult body weight. The young stayed in the nest 11-14 days, fledged at 33g (88% of adult body weight), and had a growth rate constant of 0.53. Mortality rates for eggs and nestlings were quite high, with a 63% hatching success, and only a 28% fledging success. Predation alone accounted for 44% of all mortality, most of which occurred during the nestling period. Cowbird parasitism was observed in 3 of 23 nests, and accounted for the mortality of 8% of all eggs laid.

The relatively short nestling period, rapid development rate, and light fledging weight of solitaires may be adaptations to minimize the length of the nesting period in response to the high predation pressure associated with ground-nesting.

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INTRODUCTION

The Townsend's Solitaire (Myadestes Townsendi) can be found in the western United States throughout the year. Its winter ecology has been studied in detail by Salomonson and Balda (1977) and Lederer (1977a, 1977b, 1981), but relatively little is known of its biology during the breeding season. Sullivan (1976) described the nest site of the Townsend's Solitaire as being situated on the ground on steep open slopes or on cutbanks associated with streams or roads. Although his sample size was small, Sullivan found extremely high mortality of solitaire eggs and young, only one nestling from seven nests survived to fledge. Ground nesting birds have generally been found to encounter higher mortality than similar tree nesting species (Ricklefs 1969b). Because mortality is higher for ground nesters, one would expect selection to favor a shortened nesting cycle in order to minimize the length of time that young are exposed to the high mortality. To the best of my knowledge this has not been investigated previously, but a similar problem has with regards to the development rate of hole nesting birds.

It has been known for some time that hole nesting species suffer lower mortality and, in particular, lower predation than open nesters (Nice 1957). In addition, hole nesters have been found by several authors to have slower development and longer nestling periods (von Haartman 1957, Lack 1968, Case 1978). The hypothesis presented to explain these observations is that selection pressure to shorten the

nesting cycle is less strong on hole nesters because predation rates are lower than for open nesters. The young therefore grow more slowly and stay in the relatively safe nest hole for a longer period. In contrast, Ricklefs (1969a) found no relationship between mortality and development rates in birds. He concluded that all bird species develop as rapidly as physiologically possible and that hole nesters simply stay in the nest longer after finishing development. There is no clear consensus on this matter, and further study on the relationship between nestling mortality and development rate is merited.

In addition to modification of the development rate of the young in response to predation pressure, other aspects of the breeding biology can be changed as well. Egg size could be reduced to shorten the incubation period, although presumably at the expense of development rate (see Schifferli 1973 for discussion of the effect of egg weight on subsequent development). The length of the incubation period could be shortened by increasing the percent of time the eggs are incubated, or by increasing the incubation temperature. Nestling development rate could be increased both evolutionarily by increasing metabolic rate, and behaviorally by feeding the young more often. Finally, both the age and weight at which young fledge could be reduced, resulting in less mature fledglings unable to fly proficiently, but which are relatively safe from predation by being situated away from the nest.

The purpose of this study is to describe the breeding biology of the Townsend's Solitaire, and investigate the possibility that high mortality associated with ground nesting has had an influence on the

length of the nesting cycle. To achieve this end I set out to describe nest site selection, egg sizes and egg size variation, nestling development, egg and nestling mortality rates, and adult behavior patterns. This information is then compared with data from the literature on similar-sized passerines to ascertain whether solitaires do indeed have high mortality rates, and whether this has had an influence on the various aspects of their nesting cycle.

STUDY AREA, MATERIALS, AND METHODS

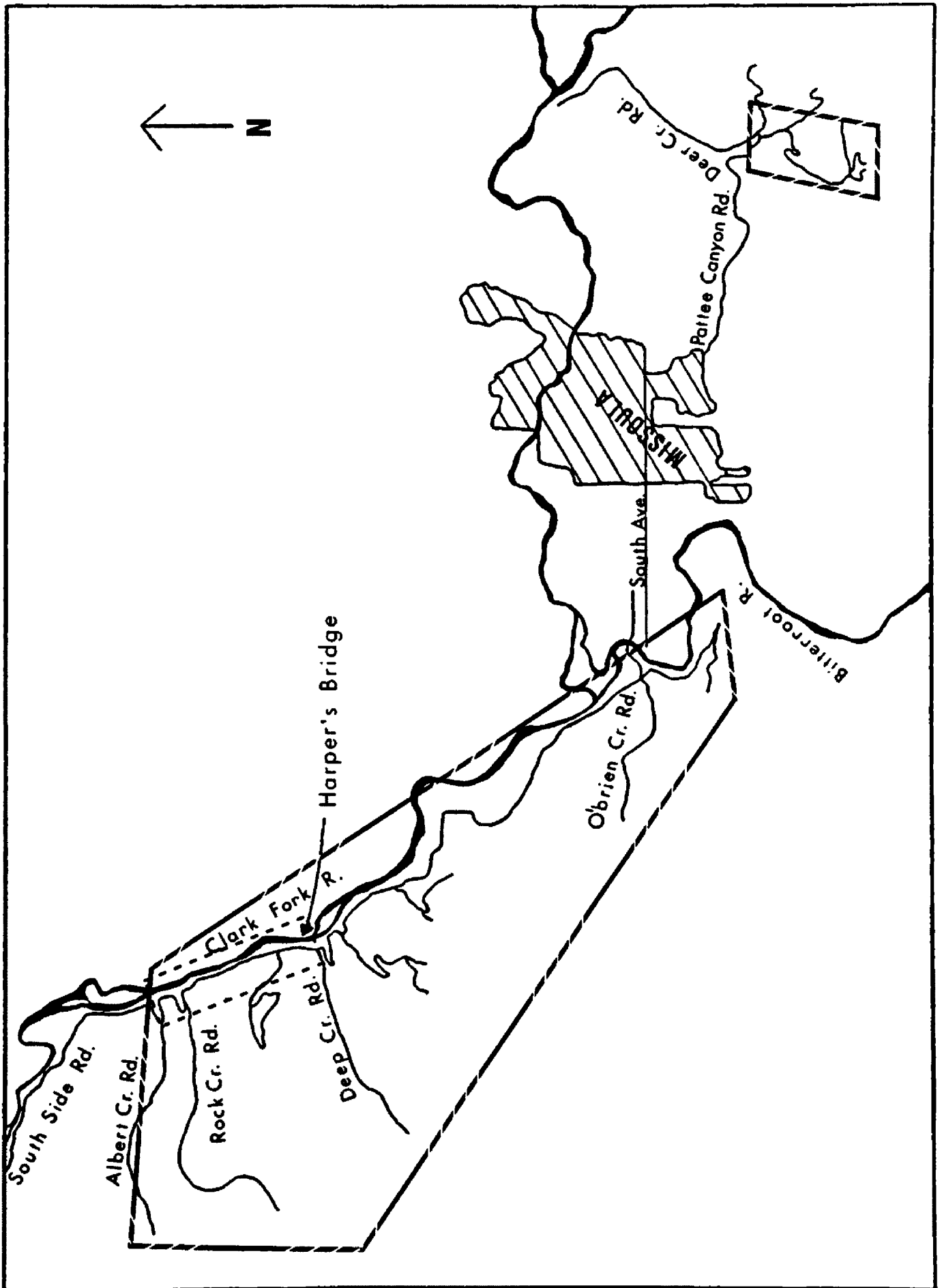
1983

In 1983 I started my search for Townsend's Solitaire nests in the area where Sullivan (1976) had previously found a nesting area. This area, the Harper's Bridge study site, was located approximately 21 km NW of Missoula, Missoula County, Montana at an elevation of 975 m (Fig. 1). Because both Sullivan (1976) and Paul (1964) indicated that solitaires seem to prefer road and stream cutbanks I concentrated my nest search efforts in those areas. The vast majority of cutbanks in this area were associated with dirt logging roads.

The Harper's Bridge study area was characterized by mixed ponderosa pine (Pinus ponderosa)/Douglas fir (Pseudotsuga menziesii) communities. Widely dispersed ponderosa pine predominated on the dry south-facing slopes, and had an understory of mixed bunchgrasses, forming a savannah-like habitat. East- and north-facing slopes were characterized by moderately dense Douglas-fir stands, with ponderosa pine also present. The understory was much more dense and complex than on south-facing slopes, with currant (Ribes cereum), chokecherry (Prunus virginiana), kinnikinnik (Arctostaphylos uva-ursi), and bunchgrasses predominating. The Harper's Bridge study site started at Harper's Bridge, and extended north along the South Side Road as far as Albert Creek Road. It included approximately 0.4 km of Rock Creek streambed, the first 0.6 km of Rock Creek Road, and the first 0.3 km of Albert Creek Road.

Figure 1. Location of study area within Missoula County, Montana.

----- 1983 study area
===== 1984 study area



Starting on 29 May, 1983 I walked and drove a total of 8 km of logging roads, plus about 0.4 km of streambed every 1-2 days, searching for solitaires or their nests. All cutbank areas were searched at least every third day throughout June. When a solitaire was spotted I followed it until it went to its nest, or until it flew out of sight. When a cutbank nest was located, I observed it from a distance using my vehicle as a blind. 8x35 binoculars and a 15-60x spotting scope were used for observations. When it was ascertained that the nest was actually an active Townsend's Solitaire nest, the precise location was noted, the nest was checked for state of completion and presence of eggs or young. Most nests were located before or during incubation.

Nest site and cutbank characteristics were analyzed in several ways in an attempt to describe the nest site. To describe the microhabitat of each nest I measured the height of the nest on the bank, height of the bank, pitch of the bank above and below the nest, amount of overhang above the nest, and direction of exposure of the bank at the nest. Nest height was measured by sighting along a meter stick, kept horizontal with a spirit level, toward a pole marked off in 0.1m increments which was placed upright at the base of the bank. Bank height was measured by recording the distance from the nest to the top of the bank with a meter stick, and adding this to the nest height. Bank pitches were measured by resting a meter stick on the bank and measuring the angle between that and the horizontal with a protractor and spirit level. The amount of overhang was measured, from the front of the nest cup, with a meter stick. The exposure of the bank was ascertained to the nearest five

degrees by placing a meter stick horizontally on the bank and measuring the orientation perpendicular to it with a magnetic compass. The above cutbank characteristics were also measured at 53 non-utilized cutbank areas. These non-use areas were selected by starting at Harper's Bridge and driving north along the South Side Rd. Every 0.1 mile (0.16 km) I stopped my vehicle and selected the most likely nest site location on a vertical cross section of the bank at that point.

Each active nest was checked daily after being found. All eggs were photographed, weighed to the nearest 0.1g with a 50g Pesola scale, and the maximum length and width were measured with dial calipers to the nearest 0.01mm. When a nest was found prior to or during egg laying, the eggs were individually marked, in the sequence they were laid, with dots of white Liquid Paper.

During incubation the females from selected nests were captured and color banded to distinguish the sexes. During the incubation period, the female was very reluctant to leave the nest. By rapidly placing a 0.4m diameter insect sweep net in front of the nest, the female would be trapped, and would fly into the net. Several attempts were made to capture males when they flew to the nest by erecting a mist net in front of the nest, but this was not very successful, and I felt disturbed both adults excessively. Nests were observed for two-hour (minimum) periods at various times during the nesting cycle to observe behavior at the nest. All observations were made from a distance of 5-15m using my vehicle as a blind. I made more detailed observations with the 15 - 60x spotting scope.

Beginning about three days before the eggs were due to hatch each nest was checked at approximately the same time of day on a daily basis. This ensured that nestlings were weighed at approximately 24-hr intervals. Each nestling was weighed in a styrofoam cup using a 50g Pesola scale. After weighing, each one was photographed next to a ruler for later analysis of development. If the eggs were in the process of hatching when checked, the nest was checked again at the end of the day and the young weighed and photographed at that time. Nestlings were weighed every day until they fledged. All nestlings were color banded around day 8. The amount of time adults spent brooding, the feeding rate of the nestlings, and the adult and nestling activity patterns were recorded during the minimum 2-hr observation periods. After the young had fledged, I searched for them daily, and if found, juvenile and adult activities were recorded. If they were not observed on three successive days after fledging they were assumed to have died or left the area, and I discontinued searching.

1984

In 1984 the Harper's Bridge study site was expanded to include many of the dirt roads from Blue Mountain north to, and including, Albert Creek Rd. (Fig. 1 and 2). Total amount of potential Townsend's Solitaire nesting habitat inspected was about 97 km of roads and trails with cutbanks. A second area, the Pattee Canyon study site, was also added in 1984 (see Fig. 1 and Fig. 3). This site included 13 km of dirt road from the junction of Pattee Canyon Road and Deer Creek Road

(1280 m) to the pass above the headwaters of Deer Creek, at an elevation of 1580 m. At the two study sites, I searched a total of 110 km of roads for nests, compared to 8 km in 1983.

Methodologies were the same as 1983 with the following exceptions. Upon hatching, each nestling was individually marked with a black permanent marker to enable an analysis of growth rates of individual nestlings. Nestlings were neither weighed nor photographed after day eight of development, when the young were color banded. After day eight I only approached the nests close enough to count the number of young present. This was because I suspected I might be inducing early fledging by disturbing the nestlings close to their fledging time.

Since territory size and characteristics were not determined, general habitat around the nest was described by measuring tree density, and per cent shrub cover, in a 0.01 ha triangular area above the bank from the nest. The 0.01 ha area was measured by pacing off, from the top of the bank above the nest, 10 m in either direction parallel to the bank, and 10 m perpendicular to the bank. Within this triangle, I recorded the number of tree trunks, and recorded per cent shrub cover, as estimated by eye. The above measurements were recorded at each 1984 nest, at each nest site previously used in 1983, and at each of the non-use locations that I was able to relocate in 1984 (44 of 53 sites).

Figure 2. Harper's Bridge study area.

x 1983 nests

o 1984 nests

1/2 inch = 1 mile

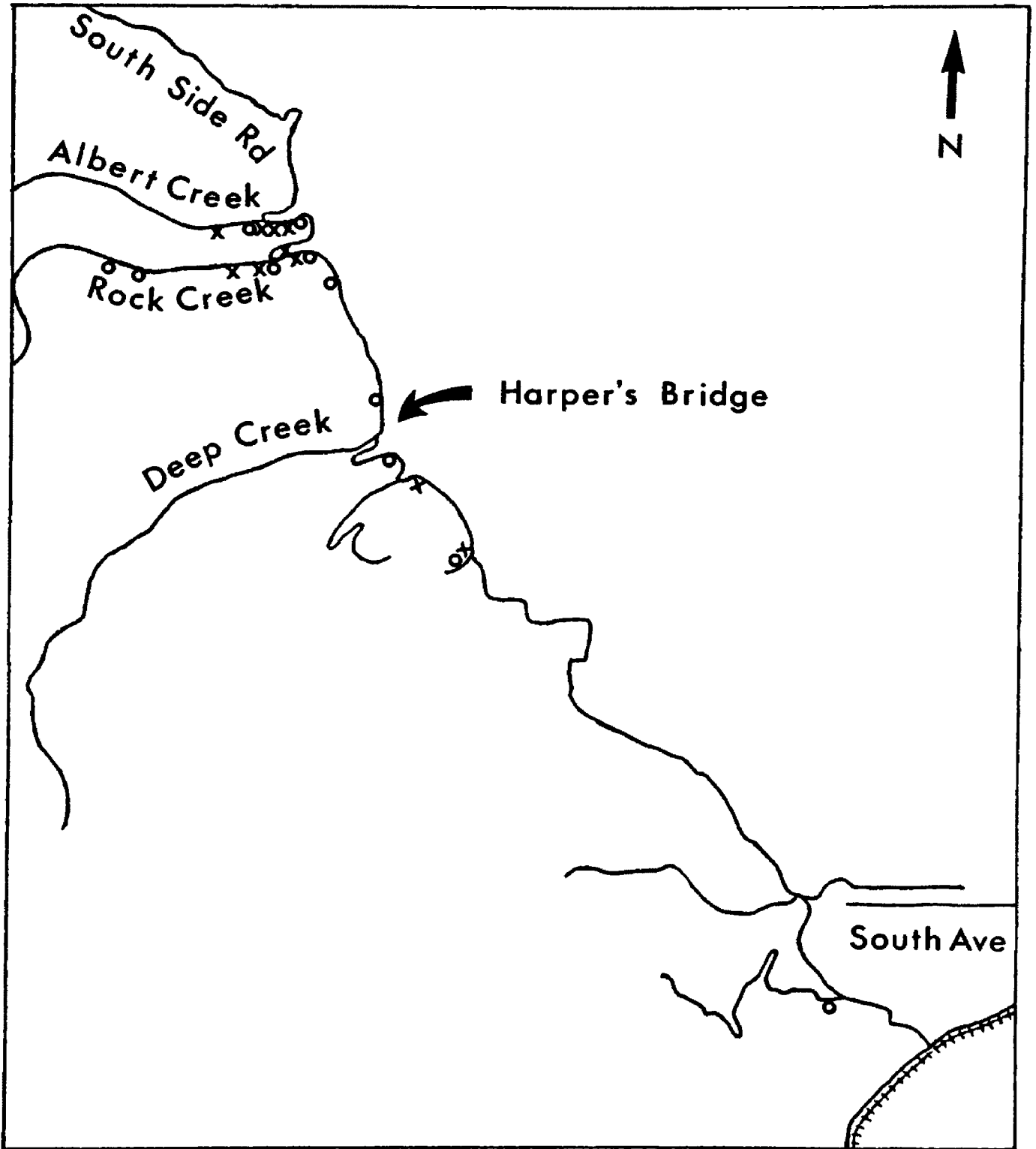
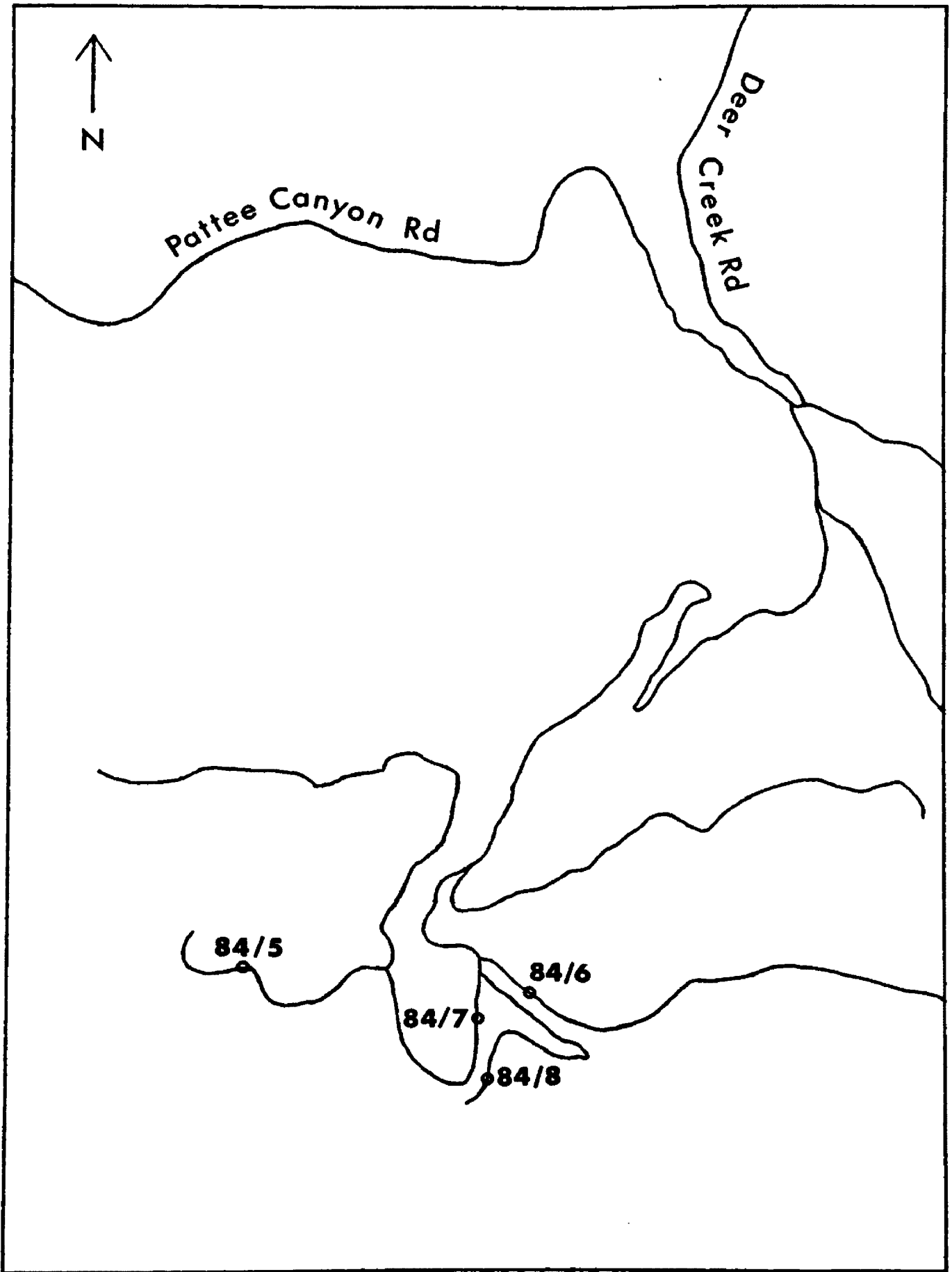


Figure 3. Pattee Canyon study area.



RESULTS AND DISCUSSION

I. Active Nests

In 1983 I found a total of 11 nests, 10 contained at least one egg, and the eleventh appeared to be an old nest. Of the 10 active nests found in 1983 four were found before, and one during egg laying, four during incubation, and one shortly after the eggs had hatched. In 1984 I located 15 nests. Thirteen were active, one was abandoned while partially built, and one was destroyed, probably after the first egg was laid (see nest 84/7 in Appendix I). Of the 13 active nests found, nine were found before egg laying had started, three during egg laying, and one during incubation. Appendix I contains a brief description and history of each nest from 1983 and 1984, and Figures 2 and 3 show the approximate locations of each nest.

II. Townsend's Solitaire Nesting Cycle

The following is a description of the nesting cycle of the Townsend's Solitaire from the time of their arrival on the breeding grounds in the spring through fledging of the young. All information is the result of personal observation, except where noted.

In 1984 solitaires arrived in the area of Rock Creek, located in

the Harper's Bridge study area, around the first of April and they were first seen in groups of 2-5. On 2 April, I observed two solitaires fly-catching near each other, one of which was singing persistently. These were the first solitaires observed in the Rock Creek area in 1984. The two did not land in the same tree for more than 2-3 seconds but there was no visible aggression. This 'pair' remained in the vicinity throughout April, but disappeared in May.

On 21 April 1984, I observed the song flight of the Townsend's Solitaire for the first time. This behavior entails a solitaire, presumably a male, ascending in large spirals to an elevation of up to 130 m while singing its regular song, then going into a dive and landing in a tree. Whittle (1922) gives a good description and diagram of this behavior. When I observed the song flight I was on the creek bed of Rock Creek, around 200 m west of the South Side Road (see Fig. 2). The solitaire was circling upward and singing until it reached an elevation of perhaps 100 m. It then flew down and to the north until I lost it in the trees. I went uphill until I reached the area where it went out of sight and I encountered a group of three solitaires. This group appeared to consist of one male and two females. One individual was singing almost constantly (hence assumed to be the male) and he repeatedly tried to approach within about 15 cm of the other two. The two non-singing individuals (presumably females) stayed more or less together while fly-catching, but never approached each other closer than approximately two meters. The females would allow the male to land in the tree with them but would fly when he tried to approach closely. The

two females gradually moved east along the hillside while feeding. The male had followed the females for approximately 150 m when a fourth solitaire appeared in the top of a ponderosa pine and started singing. The two singing solitaires perched in tree-tops about 20m apart and sang back and forth for approx. fifteen minutes. The two females continued to move east during this singing duel. I followed the females for over an hour, during which time they travelled a distance of about one km, leaving the singing solitaires behind. During this entire time period the two females did not sing or call at all.

From these and other observations I conclude that solitaires may occur in small flocks during migration, as has been described previously (Sullivan 1976). These flocks are probably mixed-sex groups but it is possible that the females migrate in flocks and the males migrate individually.

Whatever happens during migration, migratory Townsend's Solitaires typically arrive in western Montana during the month of April. When suitable habitat is found the males begin to set up territories while the females may remain together in foraging flocks during the territory establishment phase.

In general, pair formation occurs after the birds have arrived at the breeding area, although some pairs may be formed during migration. Pair formation seems to occur by a process of gradual habituation of the female to the male's approaches. The male may be attempting to courtship feed during these approaches. On several occasions I observed

males courtship feeding their mates shortly after pair formation. Courtship feeding of insects and Kinnikinnik berries were observed. Courtship feeding entails the male approaching the perched female with a piece of food visible in his mouth. The male lands near the female and gradually moves to within 15 cm of her, she then crouches down and flutters her wings in a begging posture. This begging continues while the male places the food object in the female's mouth. I did not observe copulation after bouts of courtship feeding so I assume feeding is involved in pair formation or maintenance and not mating per se. Mating was not observed during either year of this study, but Sullivan (1976) has described the copulatory display of the Townsend's Solitaire.

Both adults were involved in nest site selection, but I was unable to determine which individual initiated the activity. One member of the pair would fly to a cutbank and go under the overhang, the mate soon followed and went under the ledge as well. One solitaire, presumably the female, occasionally would crouch down and rotate as if to assure that there was sufficient room for a nest. This would last 15-30 seconds before the pair would fly a short distance down the bank and repeat the whole process. No more than three sites were ever looked at during these 'inspection tours', after which the pair would return to feeding.

Initiation of nest building was not observed, but two nests were found very soon after being started so detailed observations could be made of nest construction. At both nests only one individual was observed to be involved in nest construction. I did not try to

ascertain the sex of the nest-building bird because capturing would probably have caused nest abandonment. From observations of the nest building activities, described below, I have concluded that the solitaire involved is the female. Nest construction occurred primarily in the morning hours between 0500 and 1000 hr. The first observable sign of a future nest was a shallow depression hollowed out on the ledge where the nest would be. Twigs as long as 20cm were then dropped apparently haphazardly on the bank below the depression. This foundation was added to over the next 2-3 days until the sticks were piled above the level of the scraped depression. This left a sort of wall in front of and extending above the depression, which would later become the front of the nest.

Once the foundation was complete sticks were laid on either side of the depression and interwoven with the front wall, resulting in a U-shaped structure. Sticks were then added to form a circle of sticks surrounding the original scraped out depression. At this stage of completion the structure was almost entirely made of sticks, but some nests also included mosses and lichens. Depending on the nest site these mosses and lichens either served to make the nest quite well camouflaged, or very conspicuous to any organism with color vision.

When this stick structure was complete the nest cup itself was started. The nest cup was made primarily of dried grass, and/or ponderosa pine needles in proportions that depended upon what material was available at the nest site. In the two nests where construction was observed, dried grass was the predominant component of the nest. The

adult picked up pieces of grass from the bank, usually within 5m of the nest. When the (presumed) female had accumulated a mouthful of grass she flew to the nest and dropped the grass in or around the depression. Usually she made 2-3 such trips before settling into the cup, rotating, and apparently pushing and moving the grass with her feet. As the nest cup neared completion this behavior occurred more often. This activity pushed the grass down and against the sides until the nest cup appeared to be contoured to the female's shape, and well padded all around. The nest lining procedure took 2-3 days, in general, but females twice stopped working with the nest cup partially complete and did not resume work on their respective nests for up to two weeks. When there was no break in nest building, egg laying commenced 1-3 days after completion of the nest. The female generally spent several hours each morning on the nest during this period between nest completion and egg laying.

At nine nests, eggs were laid one per day until the clutch was complete. In four nests the female missed a day so egg laying took one more day than the number of eggs in the clutch. On three occasions this missed day occurred before the last egg was laid, and once after the second of four was laid. Eggs were generally laid in the early to mid-morning, most often between 0800 and 0900. Of 19 nests where I am relatively certain of the number of eggs laid, 2 had 3, 14 had 4, and 3 contained 5 eggs. Of the 5-egg clutches, one was used by me for an egg removal experiment so I cannot be sure how many eggs it would have had if not disturbed. If this nest is excluded, 11% were 3 egg nests, 78% were 4 egg nests, and 11% were 5 egg nests for a mean clutch size of 4.0

(SD = 0.5). A total of 74 eggs were measured over the course of two years. The average (\pm SD) dimensions were 17.3 (\pm 0.5) x 23.1 (\pm 1.1mm) with a weight of 3.7 (\pm 0.3g) (Table 1). Table 1 compares these data with data from Bent (1964) and Sullivan (1976). Using Hoyt's (1979) formula for calculating egg volume (length x width squared x 0.51), the eggs from my study had an average volume of 3.6 (\pm 0.3cc).

The females from five nests were captured and color banded while they were incubating. The purpose of the color banding was to enable me to distinguish the sexes, since they are identical in plumage. I never observed the males from these nests to incubate during the daytime, although they may have at night. From this I conclude that solitaires fit into Skutch's (1969) hummingbird pattern of incubation in which the female alone incubates the clutch. This pattern is typical of passerines. The female was observed to receive nourishment via three methods during incubation. First, the male would feed the female while she remained on the nest. Second, the male would feed the female in a nearby tree. During both of these procedures feeding occurred in a manner similar to courtship feeding. The two birds would start several cm apart, then the female begged by crouching and fluttering her wings, after which the male fed the female by regurgitation. The courtship feeding pattern was modified slightly in the second instance because the female would approach the male where he was perched, instead of the reverse. During the second feeding pattern the female was never observed to remain away from the nest for more than two minutes, she

TABLE 1. TOWNSEND'S SOLITAIRE EGG MASSES AND MEASUREMENTS

SOURCE	LENGTH(mm) ave. (range)	WIDTH(mm) ave. (range)	MASS(g) ave.
Bent(N=50)	23.5(20.8-26.5)	17.2(16.2-18.3)	---
Sullivan(N=23)	23.2(21.5-24.9)	17.1(16.6-17.9)	3.5
Shambaugh(N=74)	23.1(19.2-26.0)	17.3(15.6-18.8)	3.7
Average(N=147)	23.2(19.2-26.5)	17.2(15.6-18.8)	3.7

simply was fed and returned to the nest. The third feeding technique entailed the female leaving the nest area for up to 15 minutes. Since the female was away from the immediate area of the nest I was unable to observe her activities. These extended absences were relatively rare, perhaps as few as four times a day, during the daytime. My observations of incubating females usually lasted 2-4 hours per session. During these observation periods I observed only six complete sessions during which the female arrived, incubated and then departed. The average length of these six incubating sessions was 42 minutes (S.D.=35 min), with recesses averaging seven minutes (S.D. = 6 min). These means are most likely underestimates of the true means because short sessions will tend to be observed in full more often than long sessions. Of eleven incomplete sessions observed, for example, the average length was 89 minutes (S.D.= 48 min) with a maximum of 185 minutes.

Using the equation from Skutch (1969) for calculating incubation constancy [average length of sessions / (average length of sessions + average length of recesses) x 100] the Townsend's Solitaire had an incubation constancy of 84.5% (see Table 2). This compares with approximately 70% for other small passerines that display the "hummingbird incubation pattern" (Skutch 1969). As mentioned above, the female may stay on the nest in excess of three hours at a stretch, which is considerably longer than most small passerines (Skutch 1969). Townsend's Solitaire nests are highly prone to predation (see Sec. VIII), and this may explain the high degree of incubation constancy observed. Solitaire eggs, being white with brown spots, would be quite

conspicuous to visually oriented predators when the female is absent from the nest. The dull gray female when on the nest blends in very well with the dark conditions surrounding the nest, and may help to camouflage the eggs and nest. Because predation is high in solitaires relative to other passerines, there might be stronger selective pressure for the female to spend as much time as possible on the nest, leading to a greater incubation constancy.

Incubation in eleven nests averaged 12.2 days. Of these, 2 had an incubation period of 11 days, 5 were 12 days, and 4 were 13 days. Incubation was measured to the nearest day because the period when the young are hatching is very sensitive and I did not want to disturb the nests excessively at that time. Since egg laying, and therefore the start of incubation, and hatching both tended to occur in the morning I believe that these estimates are reasonably accurate.

Upon hatching, the young of the Townsend's Solitaire are typical for a passerine, being altricial and nidicolous. They are pink-skinned, with yellow mouth and mouth flanges and they possess a small amount of gray down on the head and back (capital and spinal pterygiae). Of seven nestlings from which I obtained both fresh egg weight and hatchling weight, the young averaged 70% (range 63-73%) of fresh egg weight. This agrees well with published weights for hatchlings of around two-thirds fresh egg weight (Welty 1975). At hatching the young weighed approximately 7% of adult body weight.

When hatched, solitaire young were quite uncoordinated, only being

able to hold their heads up for around ten seconds at a time before collapsing. The eyes were shut, with the eyes visible through the skin. There was no evidence of feathers or feather tracts (pterylae) except for the sparse down present on the back and head when hatched. An egg tooth was apparent as a knobby protuberance on the upper bill. The day the young hatch is termed day zero of development and age was counted from that point. By the age of two days the eye slits were very visible but the eyes were not yet open. The egg tooth was no longer visible. Nestling weight approximately tripled to about 19% of adult body weight by the end of this period, and all pterylae had become visible as darkened areas under the skin.

By day four of development the young were able to sit up for extended periods, although their balance was not good. The eyes were not yet open, but eye slits were clearly visible. All pterylae except the caudal pteryla had feather sheaths visible under the skin, the feather sheaths of the alar pteryla had emerged from the skin and were about 2mm long. The young now weighed about 10g or 27% of adult body weight.

During the first five days of life the female brooded the young almost continuously, whereas the male was not observed to sit on the nest. By day four the female was starting to spend some time away from the nest, but most daylight hours were still spent there. The female spent an average of 88 minutes (S.D. = 31) on the nest per brooding

TABLE 2. PERCENT OF TIME SPENT INCUBATING AND BROODING BY FEMALE.

PERIOD (days)	PERCENT OF DAYLIGHT HOURS ON NEST*
Incubation (all)	85%
Nestling (0-4)	88%
Nestling (5-9)	24%
Nestling (10-14)	0%

* calculated as [average length of sessions/(average length of sessions average length of recesses) x 100].

session, while recesses averaged 12 minutes (S.D. = 10). Using Skutch's incubation constancy equation (see above) this comes to a brooding constancy of 88% (see Table 2).

During this period both the female and the young were fed primarily by the male. Typically, the male would arrive at the nest while the female was present, he would then regurgitate one or several times for the female when she begged, before regurgitating for the young. The female would also feed the young, presumably from the food she received from the male. Sometimes the female begged for more food, and on these occasions the male would regurgitate more for her. I assume this occurred when the female had run out of food and the male was still feeding the young. The young were generally fed a viscous-looking fluid by regurgitation, but once what appeared to be a house fly was offered to the nestlings, none of the nestlings were able to swallow it so the female ate it. On several occasions small (1-2cm) light green caterpillars were fed to the young without difficulty.

The actual feeding process was initiated as soon as an adult landed on the edge of the nest, when the young reached their heads straight up with their mouths gaping open. The adult, if it had food for the young, would regurgitate or place the food item directly into the throat of a nestling. The nestling would swallow the food and very shortly thereafter turn around, stick its anus in the air and defecate. The feces of nestling solitaires are enclosed in a clear fecal sac so the adults are able to pick up and swallow or carry off the feces without leaving a mess. In addition to nest sanitation, the presence of a fecal

sac may be an important adaptation to help keep the nest camouflaged because nestling feces are predominantly bright white and would stand out dramatically in or around the nest.

At six days of age the nestlings' eyes were mostly open, and they were able to sit easily and crawl with difficulty. Most of the natal down had fallen off, but a few tufts remained. Feathers were emerging from the feather sheaths on the side and back. At this time, the young weighed about 23g, or 61% of adult weight.

By day eight the nestlings' eyes were wide open, and the young were alert and attentive to their surroundings. When placed on the ground they sat up and looked around or flapped feebly while apparently trying to escape. Feathers on all parts of the body were emerging from the feather sheaths, and were sufficient to cover most of the body. The bill flanges were becoming less prominent and the bill itself had become a dark gray-black color. Body mass of the young was approximately 28g at this time, or 75% of adult weight

During the second five days of development the female gradually spent less and less time brooding the young. The average length of brooding sessions was 25 min (S.D. = 26), while recesses averaged 77 min (S.D. = 55), for a brooding constancy of 24% (see table 2). This is somewhat misleading because brooding dropped off drastically during this period, from 48% for days 5-6 to 6% for days 8-9. I interpret this to indicate that homeothermy had developed in the nestlings by around day seven. As mentioned above, solitaire nestlings first develop an

adequate feather covering between day six and day eight, with this observation and the brooding data it is clear that homeothermy must appear at about this time (see Skutch 1976, and Welty 1975 for further discussion of the development of homeothermy in nestlings).

Feeding of the nestlings during the second five days occurred at the same rate as during the first five days. Adults fed the nestlings every thirty min (SD = 25), on average during the daylight hours. The large standard deviation reflects the fact that both adults tend to feed the young in rapid succession, with long lapses between these double feedings. For instance, at nest 84/14 on day eight, times between feedings were: 26, 8, 90, 8, 37, and 2 minutes.

Toward the end of this five day period the nestlings became quite active. They 'peeped' loudly when an adult landed on the nest to feed them, and this vocalizing often continued for up to five min after the adult left. When being fed the nestlings actually stood up and stretched their whole body toward the adult. By day nine, when I put nestlings back into the nest after weighing them they sometimes attempted to fly away, but I was always able to stop them because they were not very coordinated. Also at the end of this period, day 8 or 9, I color banded the nestlings so I could identify them after they left the nest.

By day 10 the young were well feathered, except the wings and tail, which had feathers still only partially emerged. The distinctive juvenile plumage was complete, except that the tail was still quite

short. Nestling weight had leveled off and the young weighed about 30g, or 80% of adult body weight. When the nestlings moved around in the nest they sometimes flapped their wings vigorously, as if trying to fly. They did the same thing when put on the ground to be photographed. In this way they 'ran' quite quickly while trying to escape from me. Because of this escape behavior, and associated stress, I stopped weighing the young after day 9 in 1984. I therefore have less information on the rest of the nestling period than from the previous 9 days.

When the young had reached 12 days of age they were very alert and active, and were able to leave the nest, although not fly very well. Five of the 25 nestlings which survived to fledge did so during days 10 or 11, and six more fledged on day 12. Three of these probably fledged because of my intrusions, one on day 10 or 11, one on day 11, and one on day 12. These three did not stay in the nest when I returned them after weighing. I managed to get them to stay in the nest after one or several attempts to fly away, but they were gone the next day so I assume my disturbance caused them to fledge prematurely.

When the adults arrived at the nest to feed, the young stood on the edge of the nest closest to the adult, stretched their heads and necks toward the adult, sometimes flapped their wings, and vocalized loudly. This begging behavior made the nestlings very conspicuous. The movement and vocalizations were easily noticeable from 15m away. The nestlings were often fed large objects by this age, such as caterpillars, flies, and berries.

By the end of day 14 all young had fledged, 10 fledged on day 13, and four on day 14. Of five birds for which I know time of fledging, four fledged at around dusk, the fifth fledged in mid-afternoon. Although purely speculative, fledging in the evening may be advantageous to the young because they would not be exposed immediately to the hot sun. It may also be easier for them, during this vulnerable period, to avoid predators in the dark. When the birds did leave the nest they flew from 2-40m on their first flight, depending on flying ability. Those that were unable to fly well generally ended up on or at the base of the nest bank where they were very exposed. The young weighed about 33g when they fledged, or 88% of adult weight.

In 1983 I weighed nestlings every day until they left the nest, and this may have caused all nestlings to fledge somewhat prematurely. Evidence for this is that no nestlings stayed in the nest 14 days in 1983, while four of twelve did in 1984. It may also be that 1983 was simply a better year and the young may have been better fed and therefore able to fledge sooner. Development rate data do not support this hypothesis, however (see Sec. VI and Table 5).

During the last five days that the young were in the nest (days 10-14), brooding did not occur at all (0% brooding constancy), even on cool and rainy or very hot days. The young were well feathered and apparently homeothermic without any aid from the adults, at least during the daytime. The adults fed the young somewhat more often than during the previous 10 days. On average the adults arrived to feed every 23 min (S.D. = 17), as compared with around 29 minutes for the first ten

days. This is to be expected, since the young were essentially fully grown by this time.

The young seemed to stay in the vicinity of the nest for at least two days after they fledged. They stayed more or less in the area they flew to upon fledging and were fed by the adults at that spot. I was unable to locate any fledglings after two days post-fledging, either because they were better concealed, because they left the area with the adults, because they had left the area alone, or because they had been preyed upon. I believe one of the latter three to be the case because I did not hear any fledgling vocalizations or see the adults any more after the second day.

III. BEHAVIORAL OBSERVATIONS DURING THE NESTING CYCLE

During the course of my nest observations I observed four behavior patterns exhibited by the adults that are worthy of note. These were: "broken wing display", "stretch display", "stretch flight", and "fluff pecking".

The broken wing display is a fairly common behavior pattern exhibited by female birds trying to distract intruders from their nests. This behavior, which has not been described in solitaires previously, entails the adult bird appearing to have a broken wing and fluttering along the ground away from the nest. This behavior was observed at only one solitaire nest (84/3). Each time I approached the nest when the female was present, she would flutter to the ground and run/fly across

the road with an apparent broken right wing. The first several times I observed this the ruse worked very well, and I followed the female until she got to the far side of the road where she suddenly flew away. When this activity did not succeed in keeping me away from the nest the female attacked me by flying directly toward my head. This continued as long as I was near the nest.

The stretch display was another behavior which was fairly uncommon. This activity entailed either adult perching on an exposed branch with its wings stretched upward to form a 'V'. This served to make the buffy wing patches quite conspicuous. This behavior was observed at four nests over two years (83/1, 83/2, 84/1, 84/6). On three occasions this activity appeared to occur in response to another bird species being near the nest, while four times there was no observed stimulus. On one occasion the stretch display appeared to be directed at a Rufous-sided Towhee (Pipilo eruthroptalmus) which was in the same bush as the solitaire. The solitaire repeatedly stretched its wings up while rotating 180 degrees on its perch. After doing this about eight times over several minutes it attacked the towhee and chased it away. Because of this I believe the stretch display is an aggressive display that makes the solitaire as conspicuous as possible.

Similar to this was the stretch flight, which was observed quite often as the young neared fledging age. This behavior entailed an adult flying either with very exaggerated and slow wing beats, or soaring with wings upraised as in the stretch display. Again this made the solitaire quite conspicuous, and was observed to occur during periods of

aggression. I believe this might be another threat display.

The fluff pecking behavior was observed primarily when young were present in the nest. This entailed an adult, usually the female, pecking repeatedly at the bottom of the nest cup while flapping her wings vigorously. Usually no objects were observed in the bird's mouth after these bouts, but occasionally a small object was carried away from the nest. This could be a behavior that results in the removal of fly larvae from the nest material. Dipteran larvae of the genus Protocalliphora are known to inhabit passerine nests and feed parasitically on the nestlings' blood. These larvae were observed on two solitaire nestlings during this study (see Sec. VII). I have not seen this behavior described previously, but it is logical that if this nest parasite were widespread, the birds might evolve a response intended to minimize harm to the nestlings.

IV. NEST SITE SELECTION

As mentioned previously, Townsend's Solitaires have been reported to nest almost exclusively on the ground, usually protected by an overhang above the nest. All solitaire nests located during this study were situated on cutbanks associated with past or present logging roads. Although for logistic reasons I concentrated my searches mostly along logging roads with cutbanks I believe that this is the most commonly used nesting location for solitaires in this area. In the area of the confluence of Rock Creek and the Clark Fork River I searched extensively

for nests away from logging roads in 1984. Solitaires were observed in this area prior to nesting, but once nesting had started no solitaires were observed, except those with cutbank nests associated with logging roads.

During the course of this study on nesting of the Townsend's Solitaire I collected data on nest site and non-utilized cutbank characteristics in an effort to describe suitable nesting locations. I recorded bank characteristics on 21 of 22 active nests located over the two years, plus 53 non-utilized cutbank locations. Two of the 10 active nests from 1983 were used again in 1984, although the individuals involved did not appear to be the same. Three of the eleven cutbank variables analyzed were significantly different between nest sites and non-use cutbank locations (Table 3). These were the amount of overhang above nest, exposure of bank, and pitch of bank above nest. The amount of overhang was significantly greater at used vs. non-used cutbank sites. This probably reflects the fact that solitaires require a fairly substantial 'niche' in which to locate their nests.

Non-utilized banks had a mean exposure of 42 degrees (mode = 60 degrees), while nest sites were significantly different, having a mean orientation of 349 degrees (mode = 330 degrees) (Fig. 4). There are several possible explanations for this observation. First, it may be that only banks facing NE have sufficient overhang to be suitable. This was tested by selecting only those locations with greater than 15 cm overhang. It was found that direction of exposure was still significantly different, which excludes this possibility.

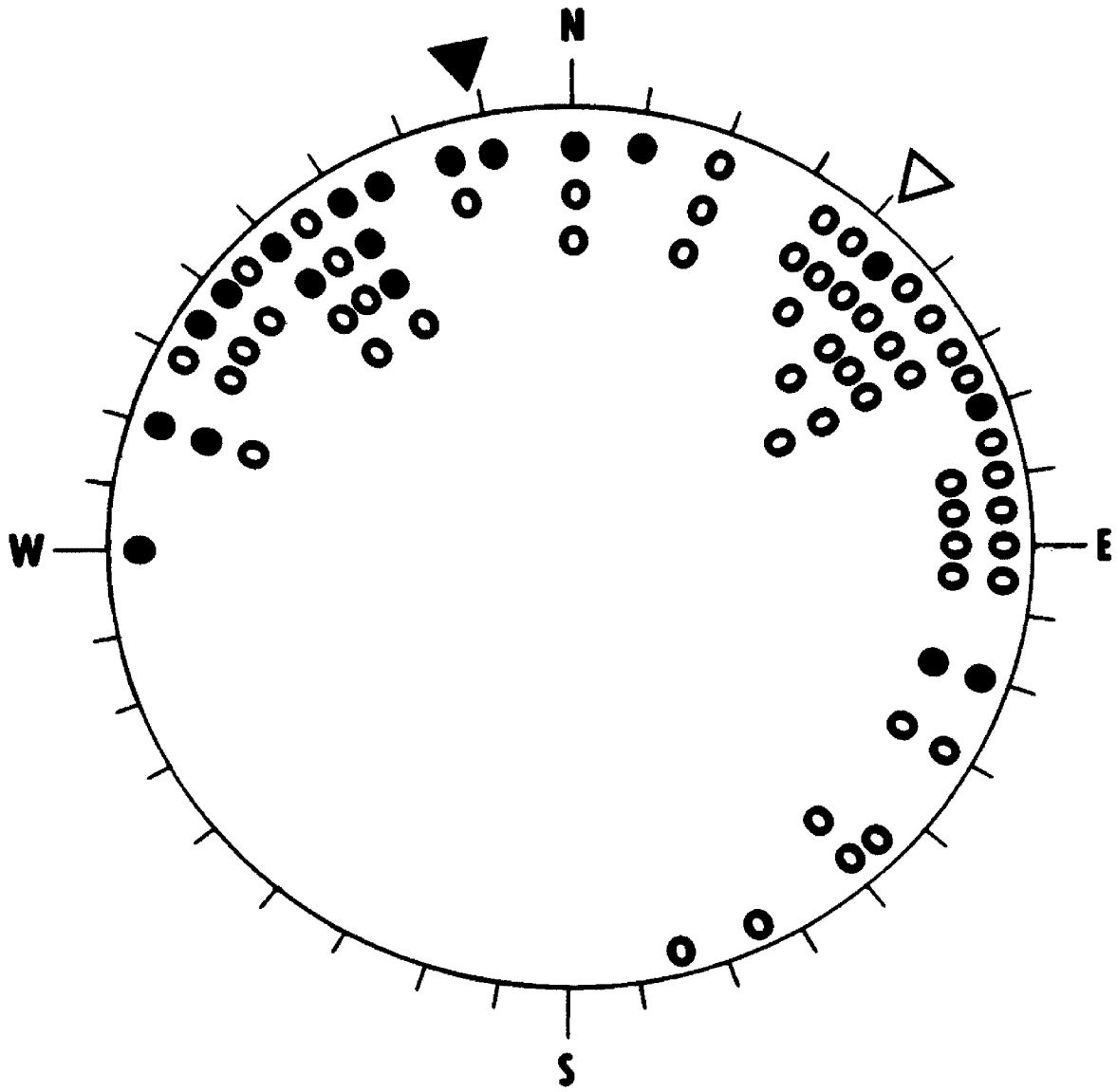
TABLE 3. CUTBANK CHARACTERISTICS.

VARIABLE	NEST SITE AVE.(N)	NON-USE AVE.(N)	T	PROBABILITY
Nest height(m)	2.66(19)	2.71(48)	0.14	0.888
Height to top(m)	0.51(19)	0.74(48)	1.29	0.200
Overhang(cm)	25.9(19)	14.8(48)	-2.39	0.020
Exposure(degrees)	349(19)	42(53)	3.29	0.002
Ave. bank pitch(degrees)	46(9)	43(52)	-0.82	0.417
Pitch below nest(degrees)	62(9)	51(48)	-1.76	0.083
Pitch above nest(degrees)	97(9)	82(48)	-2.41	0.019
Pitch above bank(degrees)	28(9)	24(48)	-0.73	0.469
Percent bare ground and moss below nest	75(19)	69(48)	-0.74	0.461
Number of trees/0.01 Ha.	11(18)	8.6(44)	-1.10	0.276
Percent shrubs/0.01 Ha.	44(18)	33(44)	-1.51	0.136

Another explanation is that solitaires select more northerly facing nest sites to avoid heat stress. Solitaire nests located on north to northwest facing banks were exposed to direct sunlight only briefly during the late afternoon, if at all. East-facing nests, on the other hand, were in direct sun for extended periods during the day, even if there was a large overhang protecting them. I believe that heat stress is the most logical explanation for the observed bank exposure selection, although I have no data to substantiate this. An interesting observation is that exposure of non-successful nests did not differ from exposure of non-used cutbanks. In other words, successful nests were significantly non-random, while non-successful nests were not. The importance of this is unknown but it may indicate that north-west facing nests are less conspicuous to predators than east facing nests.

The third variable which showed a significant difference between use and non-use sites was pitch above 'nest'. Many non-use banks did not really have suitable nest sites, so the pitch above the 'nest' was basically the same as the overall bank pitch. Actual nest sites generally had a substantial overhang above the nest and the pitch above was usually around 90 degrees (vertical). The pitch below the nest was marginally different between use and non-use sites, with nest sites being steeper (Table 3). This suggests that solitaires may be selecting nest sites which are as inaccessible as possible to terrestrial predators, or it may simply be a by-product of having a ledge present.

Figure 4. Orientation of nests (●, mean = ▼), and non-utilized cutbanks (○, mean = ▽) at the Harper's Bridge study area.



V. EGG SIZE VARIATION

I measured egg mass and size of 74 eggs from 19 nests over two years. All measurements except mass were significantly different between the two years, with 1984 measurements being smaller in all cases (Table 4). Egg mass was probably not significantly different because the precision of measurement was only to the nearest 0.1g. Egg volume was used for most analyses because it is a more precise estimate of size than any other single parameter.

To investigate the possibility that temperature during egg production had an influence on egg size I looked at weather data for 1983 and 1984. 1984 tended to be slightly cooler than 1983, with May being 1.4 C and June 1.0 C cooler in 1984. This general tendency may explain the smaller egg sizes in 1984, but temperature and egg size did not correlate well. Ojanen (1983a) found that there was a positive correlation between energy content of Great Tit (Parus major) eggs and temperature up to five days prior to egg laying, with the highest correlation at three days before. I therefore looked for correlations between mean egg volume per clutch and temperature one and three days before the first egg was laid. I used mean clutch volume because the regular intra-clutch variation (see below) would probably mask temperature effects. The best correlation found was between relative egg volume and average temperature one day before the first egg was laid ($r=-0.29$, not significant). Relative egg volume is the average for a given nest subtracted from the mean egg volume for that year. Since

this correlation was not significant no conclusions can be drawn from it except that temperature during egg formation does not have a significant impact on egg size.

Variation was also observed in egg size within both 1983 and 1984. Egg volume tended to increase throughout the season in 1983 (Fig. 5A). In 1984 egg volume gradually decreased during the length of the breeding season (Fig. 5B). In neither year was there a significant correlation between egg volume and air temperature during the egg formation period. A simple rise in temperature during the breeding season therefore does not explain the variation in egg volume as one might expect. The opposite trends in egg volume between the two years make it unlikely that any such relationship would be found.

Available food supplies should have an influence on the amount of resources a female can put into egg laying. I have no data on food availability so I cannot address this question directly. Since the Townsend's Solitaire is insectivorous during the breeding season and insect availability is generally related to air temperature (Bryant 1975), one might expect a relationship between temperature and overall physical condition of female solitaires. If a female is in better condition she will be able to lay relatively larger eggs than a female in poor condition. With this in mind I reviewed the weather data for the two years. I chose the 1984 clutch with the largest mean egg volume and searched backwards through the weather data from the date the first egg was laid until I found a relatively warm period. I found that air temperature was quite a lot higher than normal twenty days before

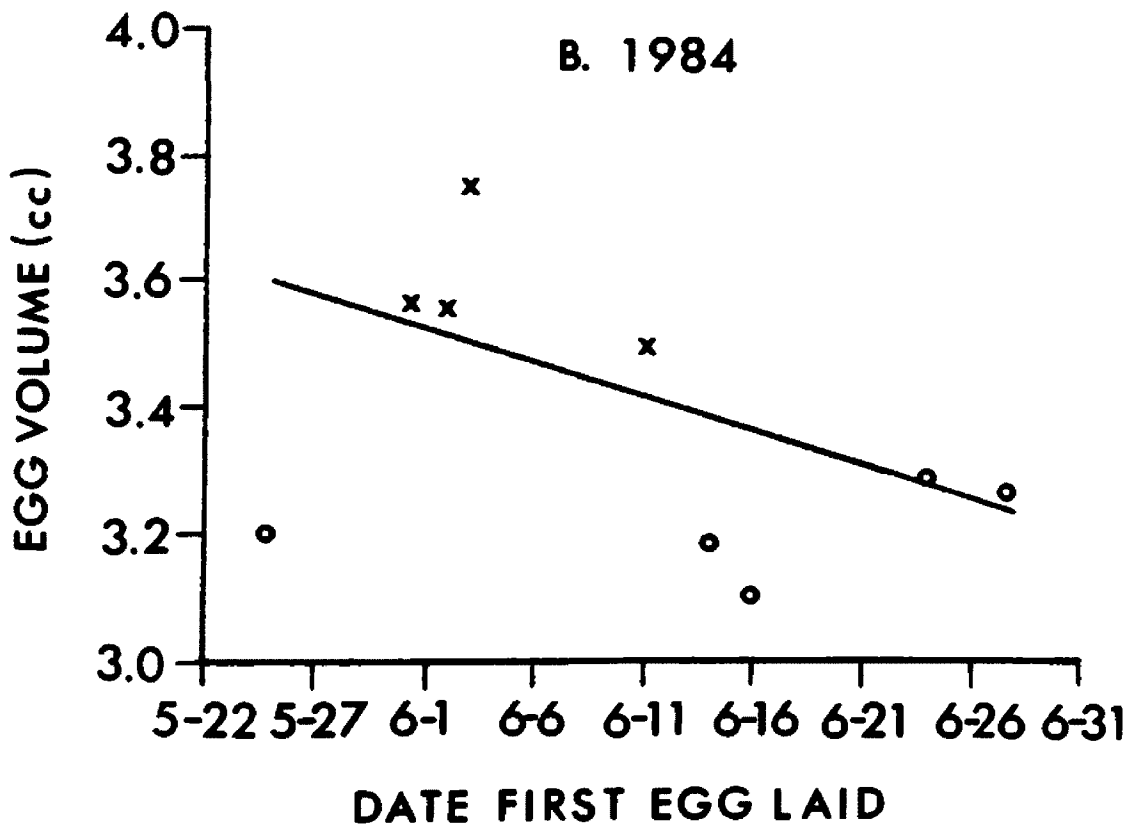
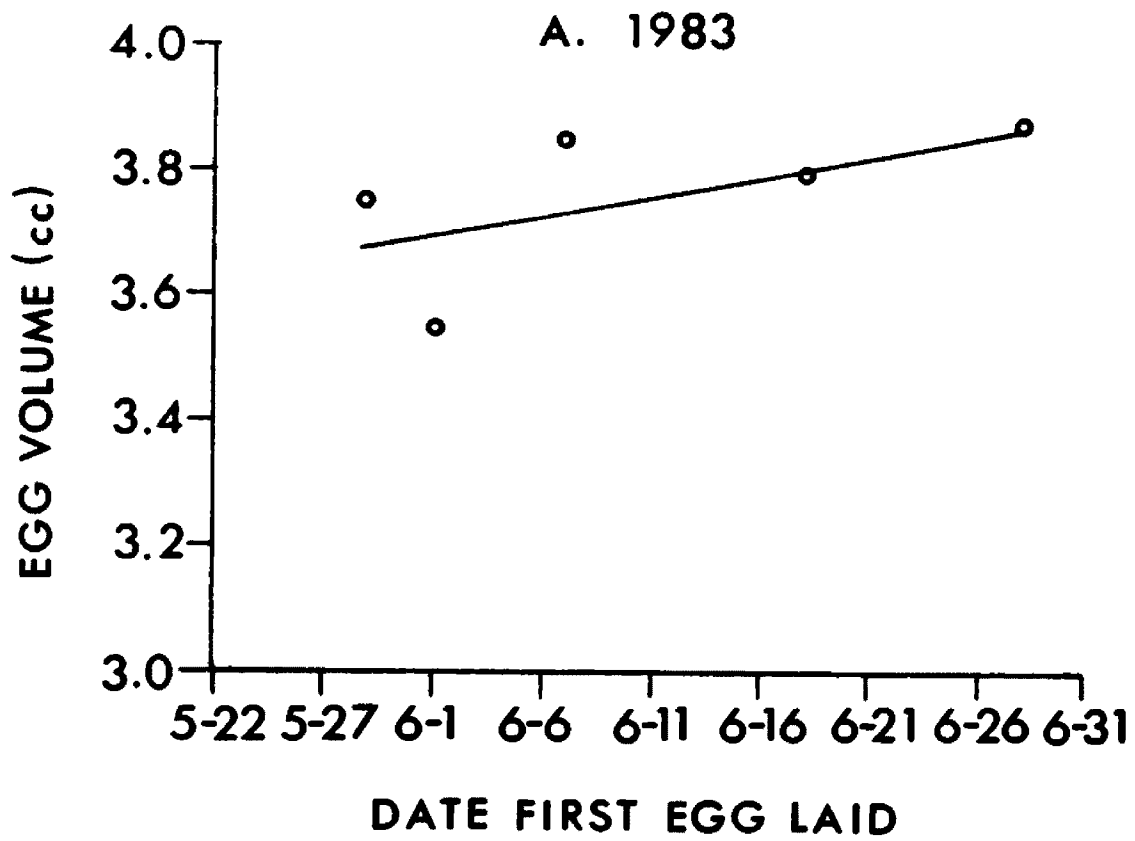
**TABLE 4. TOWNSEND'S SOLITAIRE EGG MEASUREMENTS
(with STANDARD DEVIATIONS)**

YEAR	LENGTH(mm)	WIDTH(mm)	MASS(g)	VOLUME(cc)
1983(N=24)	23.6(0.97)	17.7(0.49)	3.8(0.26)	3.77(0.27)
1984(N=50)	22.9(1.15)	17.2(0.49)	3.7(0.32)	3.45(0.29)
OVERALL	23.1(1.15)	17.3(0.55)	3.7(0.31)	3.55(0.32)

All measurements are significantly different between years except mass.

Figure 5. Relationship between egg volume and laying date.

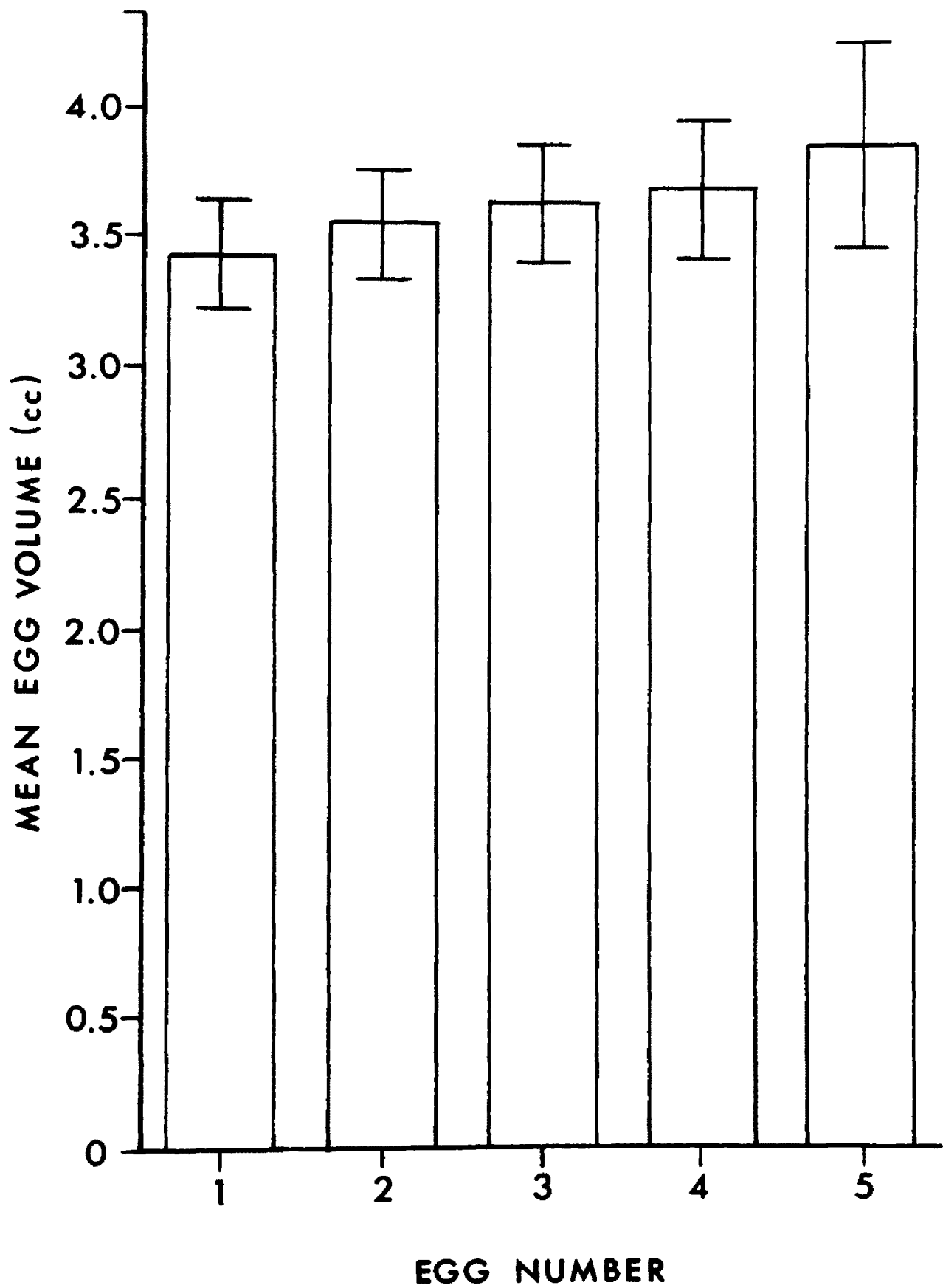
x = mean of two nests.



the largest clutch was laid. I then did a correlation between relative egg volume and temperature 20 days prior to the first egg laid for all nests in both years. The correlation coefficient for both years combined was 0.54 (N=16, $p < 0.05$) while 1983 was 0.62 (N=5, not significant) and 1984 was 0.60 (N=11, $p < 0.05$). It may be that females which experienced a warm spell about three weeks prior to egg laying were able to find more food, or feed more efficiently, than females exposed to normal or cool temperatures. They would then be able to gain additional weight and lay larger eggs.

For both 1983 and 1984 there was significant intra-clutch egg size variation. In general the first egg laid was the smallest, and egg volume increased with laying order (see Fig. 6). In 1983 I was able to get egg measurements with laying sequence on only four nests, but the trend was already obvious (Table 5). In 1984 I attempted to find as many nests as possible before egg laying to corroborate the 1983 data. The 1984 data is not as clear cut as 1983, but still 7 of 8 nests showed increasing egg size with laying sequence (Table 5). This trend is significant at the $\alpha = 0.01$ level (Friedman's $r = 16.2$) for both years combined. In general it has been found that egg size is well correlated with energy content of the egg (Ojanen 1983b), weight of the hatchling, and early growth of the nestling (Schifferli 1973). It would therefore appear that the female solitaire is investing more of her reproductive potential in the later eggs of her clutch. The pattern of having a relatively large final egg is the norm for small passerine species (Slagsvold et al. 1984). Seventeen of 21 passerines less than 50g

**Figure 6. Relationship between mean egg volume (\pm 1 S.D.)
and laying sequence.**



listed in Slagsvold et al. had a final egg larger than the mean clutch size. Also, open nesting passerines tend to have a large final egg while hole nesters have a small final egg (Slagsvold et al. 1984). The Townsend's Solitaire appears to be typical of small open nesting passerines in this respect.

In recent years there has been much discussion in the literature on parental investment strategies utilized by female birds, the most prominent of these being the brood reduction hypothesis originally put forward by Lack and Lack (1951). This hypothesis is based on the fact that for many species some hatchlings are larger, or hatch earlier, than their siblings and therefore are better fit to survive periods of food shortage. If all nestlings are of similar size and age, then they all would be likely to starve when food is scarce, whereas with the brood reduction strategy at least some will survive. Requirements for this hypothesis to be applicable to a given species are that starvation of nestlings is a prominent source of mortality, and that intra-clutch egg size variation or hatching asynchrony exists. This does not apply to the Townsend's Solitaire because even though there is egg size variation, all eggs hatch synchronously and there was little starvation of nestlings during the two years of this study (see Sec VII). I realize that two years is a short time to conclude that starvation is not an important factor in solitaire evolution, but since there was very little starvation, for only five (7%) nestlings was there evidence of starvation, and both of these years were cooler than normal, I believe it is a valid conclusion.

TABLE 5. EGG VOLUMES(cc) OF EGGS IN NESTS WITH KNOWN LAYING SEQUENCE.

YEAR	NEST	EGG NUMBER				
1983	1	3.51	3.43	3.45	3.76	
	3	3.67	3.90	3.87	4.04	
	6	3.33	3.60	3.75	4.18	4.16
	10	3.80	3.88	3.93	4.01	
1984	2	3.26	3.36	3.27	3.41	3.57
	4	3.35	3.57	3.59	3.43	
	5	3.42	3.64	3.72	3.70	
	6	3.86	3.83	3.98	3.75	
	8	3.34	3.63	3.73	3.67	
	9	3.32	3.40	3.57	3.42	
	13	3.23	3.25	3.34	3.30	
	14	3.12	3.26	3.36		
Overall mean		3.43	3.56	3.63	3.70	3.86

Other investment strategies, such as "brood survival" (Slagsvold et al 1984), and "nest failure" (Clark and Wilson 1981), are also based on hatching asynchrony. Hatching synchrony, as in the solitaire, has been associated with birds that experience high rates of predation (Clark and Wilson 1981), but see Hussell (1972) for the opposite interpretation. Synchronous hatching serves to minimize the amount of time when nestlings are present in the nest, this would be advantageous if mortality rates are high on nestlings. The Townsend's Solitaire pattern of hatching synchrony, increasing egg volume with laying order, low starvation, and high predation is not explained by any strategy in the literature. This is somewhat of a dilemma since it appears to be quite common among small open nesting passerines. The following is an hypothesis put forward as a result of my observations to explain the investment pattern in the Townsend's Solitaire. It is based on these aspects of solitaire biology: Townsend's Solitaire nests are located on the ground and are therefore accessible to both terrestrial and aerial predators. Predation on solitaire nests is the major source of offspring mortality, and predation is concentrated during the egg laying and nestling stages (see Sec. VIII). Solitaire eggs are relatively conspicuous when not covered by the female because they have an off-white background color.

EGG PREDATION HYPOTHESIS. This hypothesis begins with the observation that predation rates are highest during the egg laying and nestling periods (Sec. VIII). Apparently the presence of the female on the nest during incubation reduces the probability that the eggs will be preyed

upon. The female could therefore minimize losses during egg laying by starting incubation after the first egg is laid. With the female covering the egg(s) the nest is less conspicuous and predation should be reduced. However, asynchronous hatching of the young would result, the length of time when young are in the nest would be extended, and the chances of predation during this period would increase. Since predation rates are highest during the nestling period (see Sec. VIII) and this is the longest period in the nesting cycle, this would not be advantageous. Therefore the female should not start incubation until the last egg is laid.

By starting egg laying with relatively small eggs the female minimizes her losses if the nest is preyed upon during egg laying. For instance, if the nest is destroyed after the first egg is laid, the female will presumably have to 'dump' the second egg, but the third and fourth eggs can be resorbed. The female has then saved that amount of energy equal to the difference between the size of eggs destroyed and the mean egg size she is capable of laying. This is illustrated in Figure 7 where the sizes of eggs in four egg clutches are compared to the overall mean for these nests. Given the change in volume illustrated, there will be a net savings of energy by the female if the nest is destroyed after the first or second egg is laid, relative to what she would lose if all eggs were equal in weight. There would be no net savings after the third or fourth. By the time the female has laid her third egg she presumably cannot resorb egg number four and no savings of this sort can occur. Since some nest sites are quite

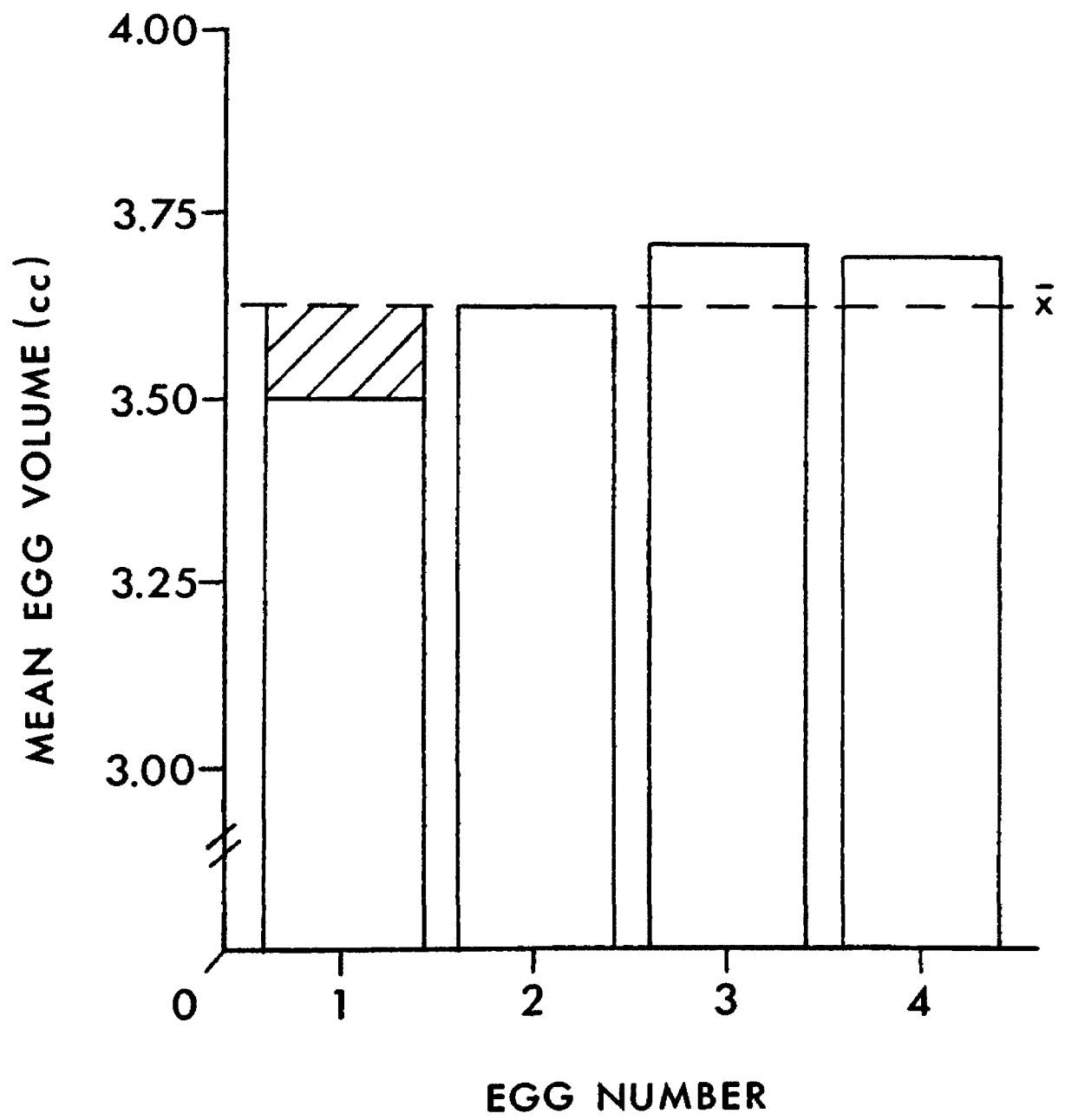
conspicuous, and the female can not know when she starts egg laying whether the nest will be preyed upon, she may be minimizing her losses if the nest is destroyed after the first or second egg is laid. If this occurs she can construct a new nest and start over, having minimized her losses.

VI. NESTLING DEVELOPMENT RATES

In 1983 I weighed every Townsend's Solitaire nestling each day until they disappeared from the nest due either to mortality or fledging. In 1984 I stopped weighing young at around nine days of age to minimize premature fledging. These data were used to analyze development rates (as per Ricklefs 1967, 1968). Ricklefs (1967) developed a technique for using weight gains to analyze growth patterns in developing birds. This technique involves plotting weight, as percent of fledging weight, versus age, then fitting this curve to one of three types of growth equation. These equations are the Logistic, Gompertz, and von Bertalanfy, and they describe sigmoid growth curves with different shapes. Once the best fit equation has been chosen it is used to convert the growth curve to a straight line. A growth rate constant (K) can then be derived from the slope of this line.

The logistic growth equation best fits the growth pattern of the Townsend's Solitaire, as it does for most passerine species. For the logistic growth equation, the growth rate is found by multiplying the slope by four (Fig. 8). I was able to get at least five days of weight

Figure 7. Relative savings (shaded area) obtained by laying a small first egg for the Townsend's Solitaire (see text for explanation).



values for a total of eleven nests, five in 1983 and six in 1984. In 1983 the overall development rate was found to be 0.51, while in 1984 it was 0.53. For all nestlings combined for both years, the rate constant equaled 0.53 (Table 6). The nestling from nest 84/14 was not included in these calculations because it had ectoparasites and grew abnormally slowly (see Table 6 and Sec VII). For each of these average rate constants, data were utilized from days zero thru nine only. The reason for this is that early development is the most representative of the true rate (Ricklefs 1967). A small change in weight late in development causes a large change in the converted value, and therefore has a large influence on the slope of the line (Figs. 8 and 9). There is a large amount of variation in development rates among nests (range = 0.48-0.64; Table 6). This variability is due to factors such as number of nestlings in a nest, presence of parasites, hatching date, and possibly egg size and food availability.

An analysis of development rates in nests with four nestlings ($n = 7$, omitting 83/6, 84/3, and 84/14) shows a clear trend of decreasing development rate through the breeding season (Fig. 10). Whether this is a true relationship between rate and date, or due to other factors such as food availability or egg size, is unknown. I have no estimate of food supplies so I am unable to discuss this hypothesis. Unfortunately I have both egg size and development rate data for only four of these nests, but for these there is a strong negative correlation (Fig. 11). This relationship might be expected because in

**Figure 8. Relationship between growth curve
and derived development rate.**

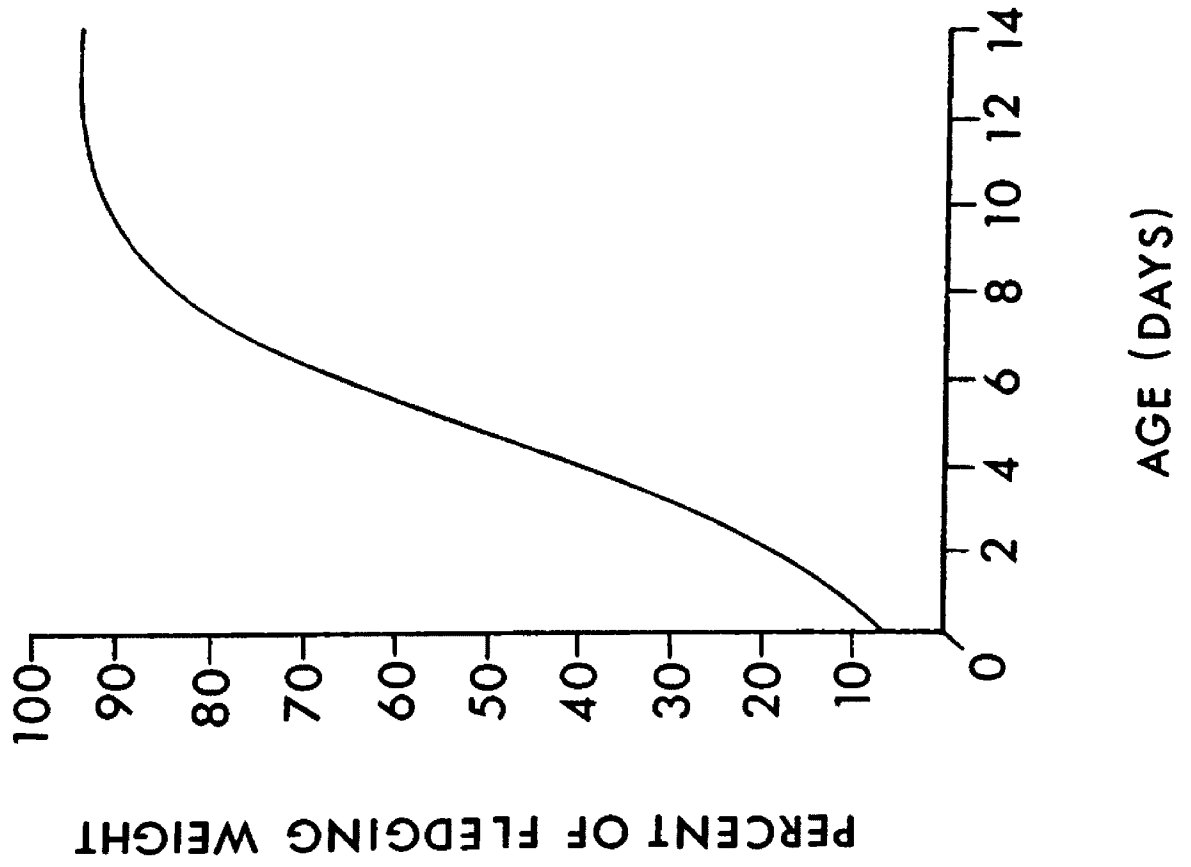
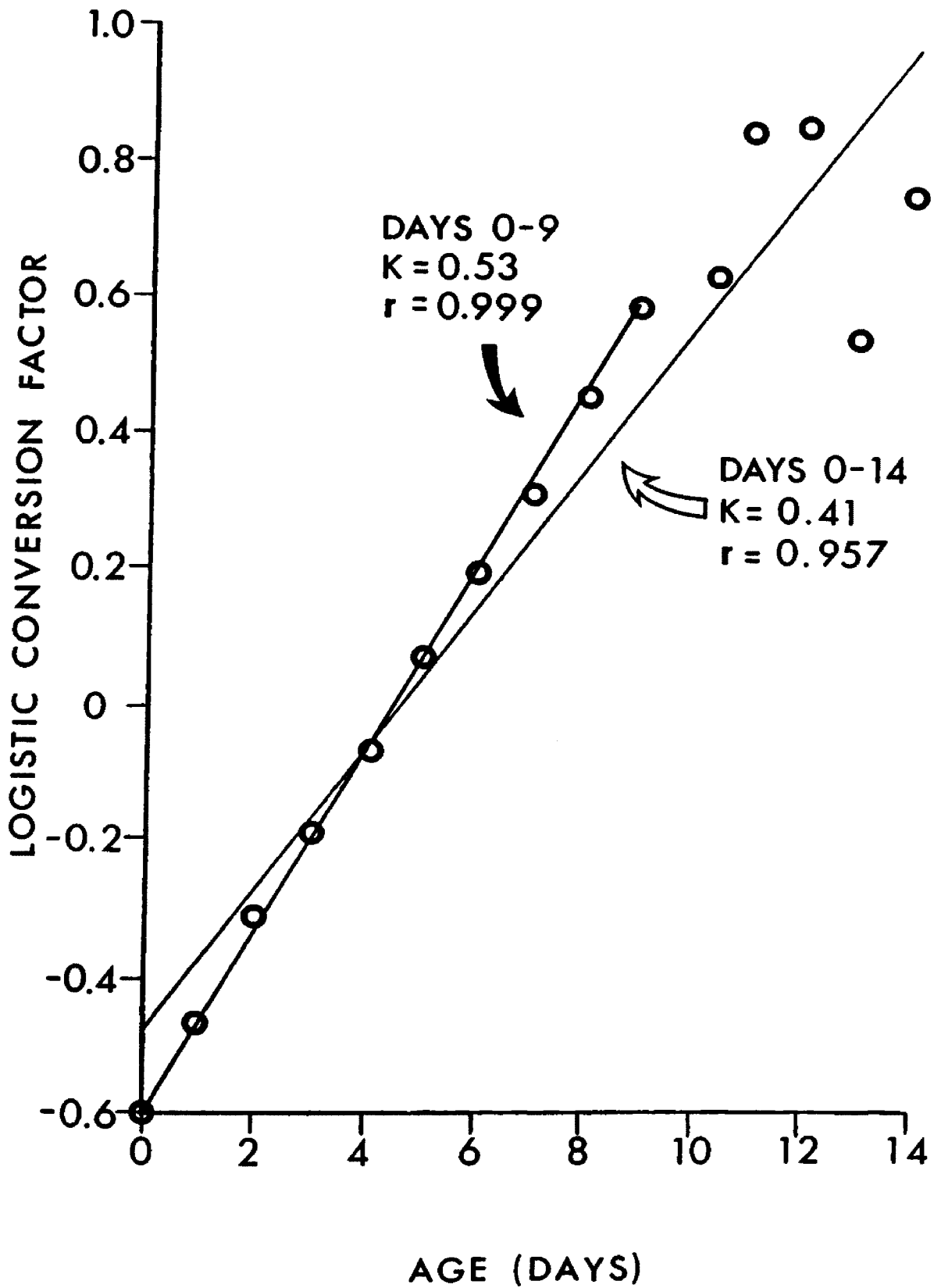


TABLE 6. NESTLING DEVELOPMENT RATES.*

NEST	A	K	r	HATCH DATE	NUMBER OF HATCHLINGS
1983					
83/2	32	0.56	0.999	5/30	4
83/3	34	0.49	0.995	6/22	4
83/6	33	0.64	0.989	7/5	1
83/7	32	0.58	0.998	6/1	4
average	34	0.51	0.996		
1984					
84/1	34	0.53	0.999	6/9	4
84/3	33	0.49	0.998	6/15	5 -> 1
84/6	33	0.48	0.993	6/19	4
84/8	35	0.50	0.987	6/17	4
84/13	35	0.59	0.999	7/10	2
84/14	26	0.48	0.996	7/12	1
average	33	0.53	0.999		
Overall average	33	0.53	0.999		

* A= asymptote of growth curve (approximately equal to fledging weight).
 K= logistic growth curve rate constant. r= correlation coefficient of
 linearized growth curve.

**Figure 9. Comparison of growth rate derived from
days 0-9 with days 0-14.**



clutches with large eggs the young start out larger, cannot gain weight as rapidly, and do not 'need' to grow as rapidly to reach fledging weight in the same amount of time. Associated with this last point, nestlings hatching from larger eggs did not fledge at a heavier weight. The data for both of the above analyses are very limited so it is impossible to say conclusively what is occurring. Previous studies have found development to be more rapid late in the season (see Ricklefs (1968) for a review). For this reason I believe that the sharp decrease in development rate through the breeding season is not simply due to hatching date.

Within a given brood, the individual nestlings grow at very similar rates. The nestlings from a representative nest for which I have sufficient data to analyze individual growth rates (nest 84/1) had rate constants of 0.526, 0.534, 0.538, and 0.543 (S.D. = 0.006). This compares with a standard deviation for all nests of 0.055. This is to be expected in a situation where nestling competition is not severe.

Ricklefs (1968) reviewed the literature on development rates in nestling birds. Using his data for other passerines, I found that solitaires grow slightly faster than similar-sized passerines ($t = 1.99$, $p < 0.10$). If one compares solitaire development rates with similar-sized ground nesting passerines the rates are similar. This may be related to the fact that mortality rates are higher for ground nesting birds (Ricklefs 1969a), and may indicate that the length of the nestling period has become shortened due to unusually strong selective pressure.

Figure 10. Change in development rate through the season.

● 1983

x 1984

○ nests included in regression

(four egg nests).

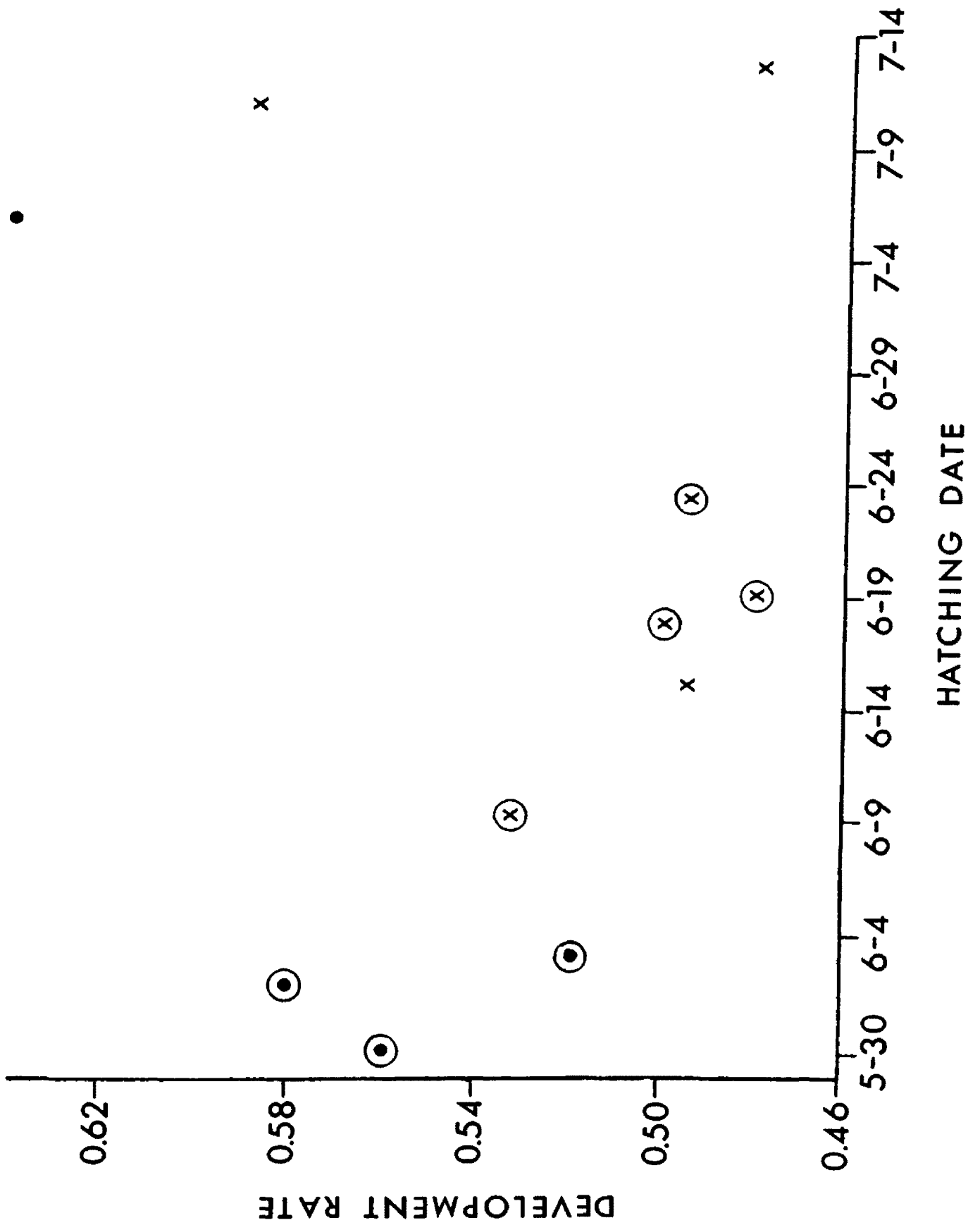
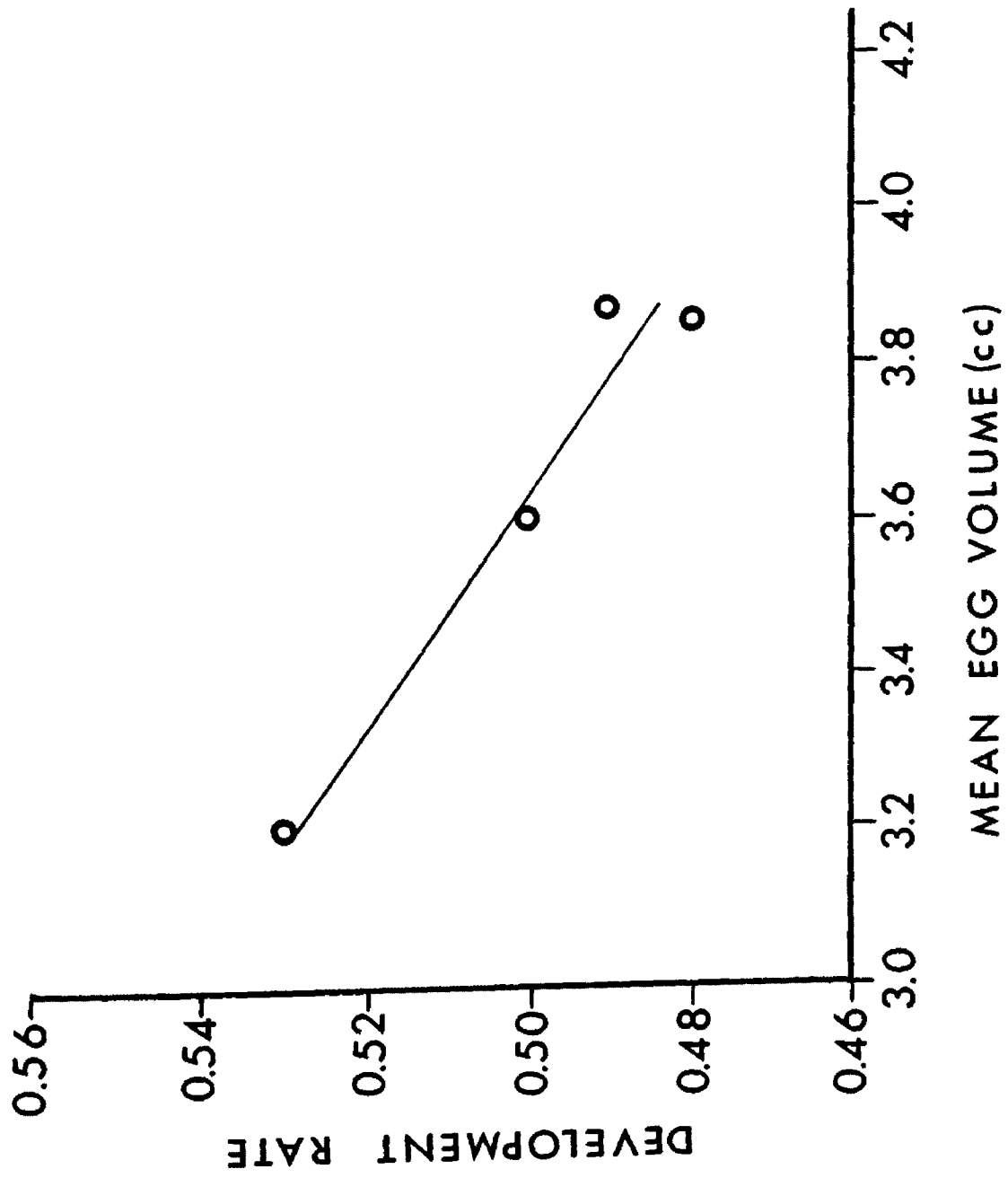
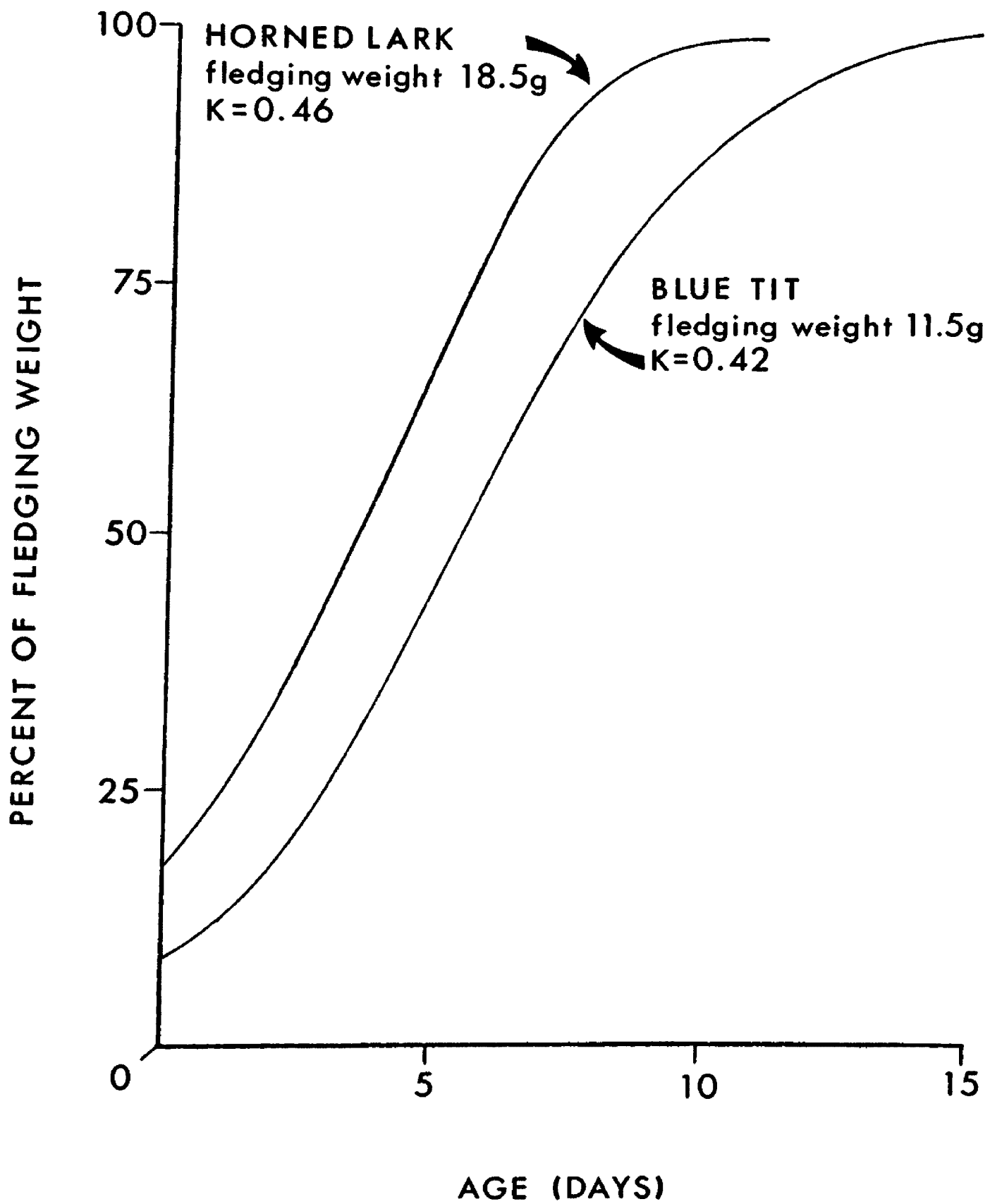


Figure 11. Relationship between development rate and egg volume.



It has been observed by several authors that growth rate is inversely correlated with body size. Williams (1966) observed that large birds generally suffer lower mortality than small birds, and suggests that differential mortality rates may be the cause of the variability in growth rates of animals in general. One of the classic examples used to illustrate this phenomenon is the comparison of hole-nesting versus open-nesting passerines. Hole-nesters suffer much lower mortality, especially predation, than open-nesters, and generally have slower developments and longer nestling periods (Nice 1957, Case 1978, von Haartman 1957). For example, von Haartman (1957) compared development of a typical open-nester with a hole-nester. The open-nester, even though it weighs 70% more at fledging, grows 10% faster than the hole-nester (Fig.12). Ricklefs (1969a) tested the above hypothesis and found no correlation between growth rate and mortality rate. He found that virtually all of the variability in growth rate can be attributed simply to differences in adult body weight ($r^2 = 0.85$). He concluded that the physiology of growth for different sized organisms limits the rate at which they can grow. According to this theory virtually all altricial birds are developing as quickly as physiologically possible. Ricklefs (1968) conceded that hole-nesters develop more slowly than open-nesters, but found no evidence for a general relationship between mortality and growth rate.

Figure 12. Comparison of growth curve of open-nester
and hole-nester (modified from von Haartman 1957).



As pointed out by Case (1978), a potential problem with Ricklef's analysis is that mortality rates and development rates are not necessarily from the same population. Also, the mortality rates used are basically instantaneous rates for a single population. They may bear no relationship to predation pressure over evolutionary time. This is of course impossible to assess, and holds for all analyses of mortality rates, but it is worthy of note.

Ricklefs (1968) found that most (19 out of 25) passerines which fledge at less than 90% of adult body weight are ground feeding birds. He speculates that this is because they do not need to be adept flyers to catch prey, so they can fledge at a relatively immature stage. This explains the relatively light fledging weight of solitaires (approx. 88% of adult body weight) , but it does not explain the rapid development. Adult solitaires at the Harper's Bridge area feed primarily by perching on a low branch and flying down to the ground to catch prey (Sullivan 1976). It is possible that fledglings secure prey from the same location, but stay on the ground while doing so.

VII. PARASITISM

There were two types of parasitism observed in the Townsend's Solitaire population under study, larval insect ectoparasites and vertebrate nest parasites (Brown-headed Cowbirds, Molothrus ater). Ectoparasites were observed on two nestlings, one in 1983 and one in 1984. In 1983 one insect larva was found on a 7 day old nestling from

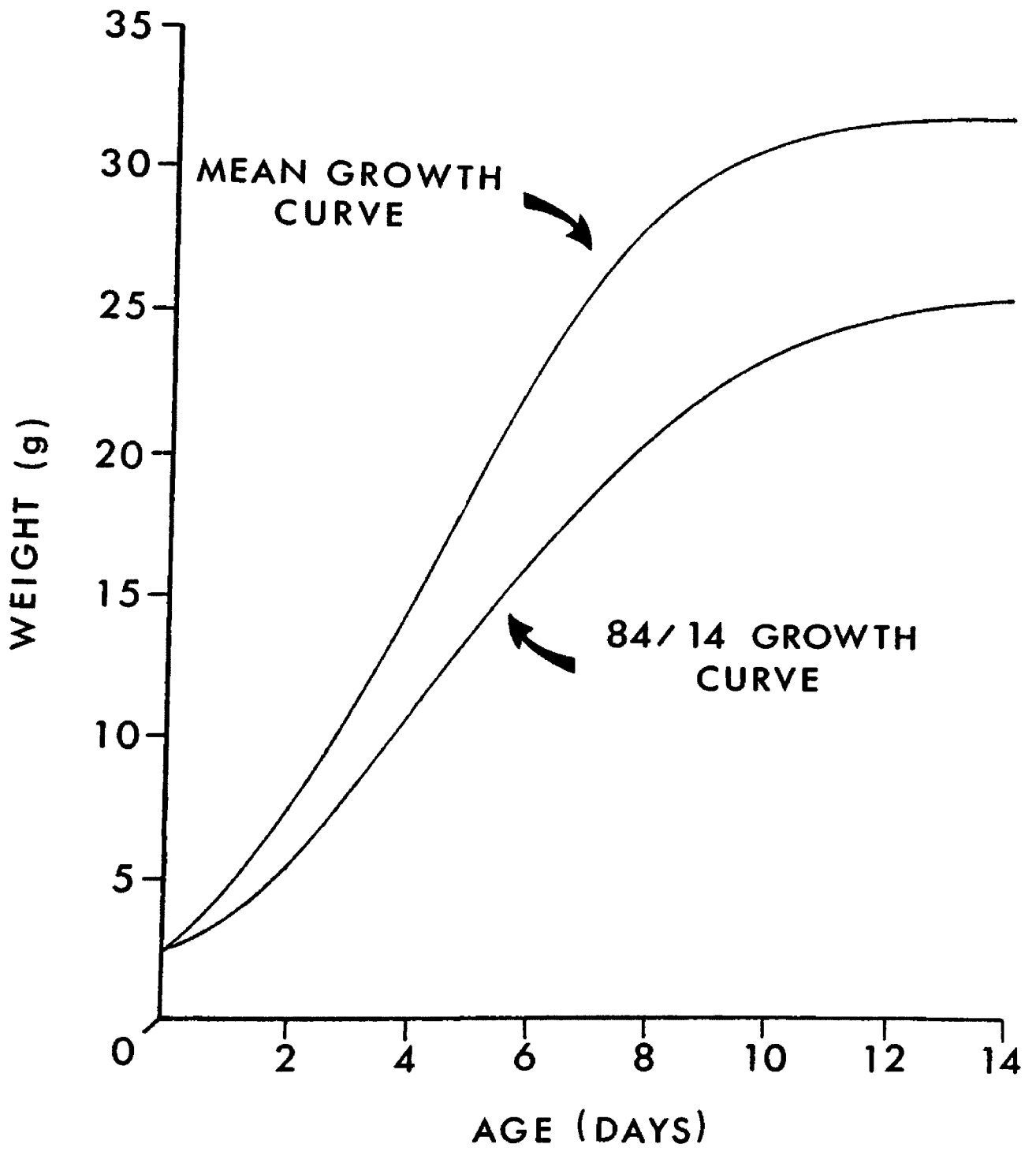
nest 83/2. The larva was an off-white color, showing no evidence of 'blood sucking', and was situated on bare skin on the back above the anus. I removed the larva, it was not burrowed into the skin at all, and gave it to Dr. J. Bromenshenk (Zoology Dept. Univ. of MT) for identification. It was found to be a Dipteran larva of the genus Protocalliphora. No other larvae were found on this nestling or its siblings, and it showed no adverse affects. This type of ectoparasite is fairly common in passerine nests, sometimes causing no harm while at others causing mortality. Allen et al. (1952) observed a Purple Martin (Progne subis) nest where all four nestlings had died. Upon inspection of the nest they found 294 Protocalliphora splendida larvae weighing 21.5g or about 20% of the combined nestling weight when they died. Arnold (1919) stated that Protocalliphora sp. larvae burrow into the skin anywhere on the body other than the legs, while Pletsch (1948) found larvae in the nares of a nestling Black-billed Magpie (Pica pica). Welty (1975) stated that the larvae of these flies are primarily found in nests of hole nesting birds. Apparently, adult flies lay their eggs in a nest and when the larvae hatch they spend the daylight hours in the nest material and migrate up onto the nestlings at night to feed by blood sucking. This is the most common description of their habits, although Arnold found the larvae staying burrowed into the skin of nestlings until the nestling died. The species designation of members of this genus does not seem well defined so it may be that Arnold was observing a species with a slightly different life history than most.

In 1984 the one nestling present in nest 84/14 had a heavy

infestation of fly larvae. At an age of one day the nestling had what appeared to be dried blood in the ear openings. The next day one larva was observed on its neck and upon closer inspection 10-15 larvae were found under each wing. All larvae had dark red inside their digestive tracts, so they had apparently been ingesting blood from the nestling. Two larvae were collected, but they died immediately so a positive identification was not possible, but they were presumably Protocalliphora sp. larvae. On day three there was no superficial evidence of larvae on the nestling, but dried blood was still present in one ear canal. It may be that the larvae burrowed into the skin as Arnold (1919) observed and I simply did not see the "pits", or the larvae were not on the nestling because it was daytime. In either case the nestling appeared to continue to be affected by the parasites because he grew more slowly and fledged at a lighter weight than any other nestling (see Table 6, and Fig. 13).

The second type of parasitism observed was Brown-headed Cowbird parasitism. One nest was parasitized in 1983 (83/6), and two in 1984 (84/9 and 84/11). In nest 83/6 the female solitaire laid one egg on each of the first two days of egg laying, by the third day egg number one had disappeared and the female had laid a third egg. On day four egg number two had disappeared, the solitaire had laid a fourth egg, and a cowbird egg was present. The second solitaire egg to disappear was found with a hole in it at the base of the bank below the nest. On the

Figure 13. Comparison of 84/14 nestling growth curve with mean growth curve.



fifth day of egg laying the female solitaire had laid a fifth egg, to complete the clutch. The female then commenced to incubate the three solitaire eggs and one cowbird egg. The cowbird hatched after 11 days of incubation, one solitaire hatched 13 and one 14 days after incubation started. The third solitaire egg did not hatch and disappeared one day after the last nestling hatched. Whether this last egg was not viable and was removed by the female solitaire or if it was pushed out by the young cowbird is unknown. The second solitaire to hatch grew more slowly than the other nestlings and disappeared when eight days old. This nestling presumably starved but its actual fate is unknown.

The chronology of nest 84/9 is similar to that related above. Again, the female solitaire laid two eggs before a cowbird removed one egg. The egg was removed the same morning that it was laid. The next day the female laid a third solitaire egg. On day four of egg laying the third egg had disappeared, a fourth egg had been laid, and a cowbird egg was present. The female solitaire started incubating two solitaire eggs and one cowbird egg at this point. The next day one of the solitaire eggs disappeared between 0800 and 0900 hr. Somehow the adult cowbird must have flushed the incubating female off the nest long enough to remove an egg. Both the solitaire and the cowbird hatched after an incubation period of 12 days. Both nestlings disappeared when 3-4 days old, presumably succumbing to an unknown predator (see Sec. VIII).

Nest 84/11 was found when the female was incubating three solitaire eggs and one cowbird egg. The cowbird egg hatched five days after I found the nest, and the first solitaire hatched the next day. The

second solitaire egg hatched the day after that. Solitaire egg 3 was abnormally small and never hatched. The nest was found deserted the next day (see Sec. VIII).

The above descriptions of cowbird parasitism are the first recorded cases of this phenomenon in the Townsend's Solitaire. This is probably not because it is a new phenomenon, but because the solitaire has not been studied in sufficient detail. Paul (1964) on the other hand observed 75 solitaire nests over 14 years and never saw a cowbird egg present, even though cowbirds were present in the area.

The observed cowbird parasitism of solitaire nests occurred in a manner typical of cowbirds. One or two solitaire eggs were removed from each nest before the cowbird laid her own single egg in the nest. Freidmann (1963) stated that Brown-headed Cowbird females generally remove one or two eggs either before or after they lay their own egg(s) in the nest. He also notes that nests with more than one cowbird egg are as common as single-egg nests, although this was not the case at the limited number of solitaire nests observed. Friedmann also found that cowbird females mostly lay their eggs before dawn, whereas a cowbird laid an egg in a solitaire nest between 0800 and 0900 hr during this study. Interestingly, this is also the time period when most solitaire eggs were laid (see Sec. I).

In 1981 a study of Western Flycatcher (Empidonax difficilis) nesting was undertaken in the Harper's Bridge area (Dolan and Wright 1984). It was found that Western Flycatchers, which are slightly

smaller than solitaires, were nesting in the same cutbank areas as solitaires. This flycatcher population was found to have 42% of its nests parasitized by cowbirds, compared to 13% for solitaires. This discrepancy may be due either to the size difference or nest availability, flycatcher nests were more numerous.

VIII. MORTALITY

In the Townsend's Solitaire population that I studied mortality rates were quite high. Of 88 eggs laid, 55 hatched (63%), and 25 fledged (28%). Nice (1957) reviewed the literature on nesting success in open nesting altricial birds. She found average hatching and fledging successes of 60% and 46% respectively. From this it can be seen that hatching success in the solitaire is approximately normal but nestlings had a relatively poor chance of survival.

Predation is by far the most important source of mortality in solitaires (32% of eggs laid, 44% of total mortality) (Table 7). Predation was assumed to have occurred when all eggs or nestlings disappeared simultaneously. Actual predation was never observed, but on one occasion adult solitaire feathers were found scattered around the nest (83/1), and a hawk (*Buteo* sp.) breast feather was found below another nest (84/8). Of the other six nests lost to predation, two were found torn apart while four were totally intact. The destroyed nests were probably preyed upon by mammalian predators while the intact ones may have been lost to avian or small mammal predators. One nest which

was found destroyed has not been included in Table 6. I had been keeping track of this nest (84/7) but I never observed any eggs actually in it. It may have been destroyed soon after the first egg was laid or possibly a predator destroyed it looking for non-existent eggs.

Three of the 22 active nests found were deserted by the adults. Nest 84/2 was used for an egg removal experiment to ascertain if solitaires are determinant layers. After the second egg in this nest was laid I removed one egg per day until the female stopped laying (the female laid a total of five eggs). The female abandoned the nest five days into incubation. It is possible the female deserted due to my activities but one might expect her to desert during the experiment, not five days later. Nest 83/9 was found with the female incubating three eggs. I captured and banded her three days later and she deserted five days after that. Capturing her may have stressed her sufficiently to make her abandon the nest, but again it would be expected that this would occur soon after my disruption not five days later. Another explanation is that the eggs were infertile and the female abandoned for this reason. Since I found this nest during incubation I have no way of knowing how long the female had been incubating before she abandoned.

The third abandoned nest (84/11) was a cowbird parasitized nest. When found, the female was incubating one cowbird and three solitaire eggs. The cowbird hatched five days later, two solitaires hatched one and two days after that, and the third solitaire egg never hatched. The

TABLE 7. NUMBER OF YOUNG (NESTS) LOST TO THE MAJOR SOURCES OF MORTALITY DURING THE THREE PHASES OF THE NESTING CYCLE.

SOURCE	PERIOD IN NESTING CYCLE			TOTAL MORTALITY	PERCENT OF TOTAL MORTALITY	PERCENT OF EGGS LAID
	EGG LAYING	INCUBATION	NESTLING			
Predation	4(2)	6(2)	18(5)	28(8)*	44	32
Desertion	0(0)	8(2)	2(1)	10(3)	16	11
Cowbird parasitism	5(3)	1(1)	1(1)	7(3)	11	8
Starvation	0(0)	0(0)	5(2)	5(2)	8	7
Hatching failure	0(0)	2(2)	0(0)	2(2)	3	2
Other	2(1)	5(2)	4(1)	11(4)	17	14
Total Mortality	11(6)	22(9)	30(10)	63(18)		
Total Mortality, percent of eggs laid	13	25	34			72
Percent Mortality per day**	4.3	2.1	2.6	2.6		
Instantaneous Mortality***	4.5	2.8	6.1	4.5		

* Row totals for number of nests do not necessarily equal sum of column values because some nests experienced mortality during more than one per
 ** Percent mortality per period/length of period.
 *** See text and Ricklefs (1969b)

day after the second solitaire hatched one nestling was found dead about 30cm below the nest and the other two were, apparently, dead in the nest. The solitaire nestling found "dead" in the nest revived somewhat after I collected it, but I was unable to keep it alive, and it died several hours later. This nestling was cold to the touch when I collected it, but it still managed to "wake up" for a short time before it died. Several possible explanations exist for this nestling desertion. First, it could be that my activities disturbed the female enough that she deserted. I do not believe this to be the case because solitaire females seem quite tenacious once there are young in the nest. Another explanation is that the female abandoned because one of the nestlings fell out of the nest. This may have been an accident or the cowbird may have pushed the nestling out. In either case a nest with a dead decaying nestling on the bank below it is probably much more likely to be preyed upon than a normal nest. This is evidenced by nest 83/7 where the nestlings were preyed upon within 24 hours of a nestling falling from the nest. If a female knows this it could be a cause for abandonment. A third possibility is that the female deserted because of the presence of the cowbird chick. The females from two other cowbird parasitized nests did not abandon due to a strange chick in the nest, but it is still a possibility. Finally, the female may have deserted this nest because one of the eggs failed to hatch. This is not common among passerines and did not occur at nest 84/8 where an egg failed to hatch. It is not possible to distinguish which of these is the correct explanation, in part because it is unknown whether the nestling fell out of the nest before or after the female abandoned. It is also possible

that the female died away from the nest.

The third major source of mortality in solitaires was Brown-headed Cowbird parasitism, which has been discussed in detail above (see Sec VII). It is sufficient to note that most of this mortality occurred during the egg laying period and was presumably caused by the female cowbird.

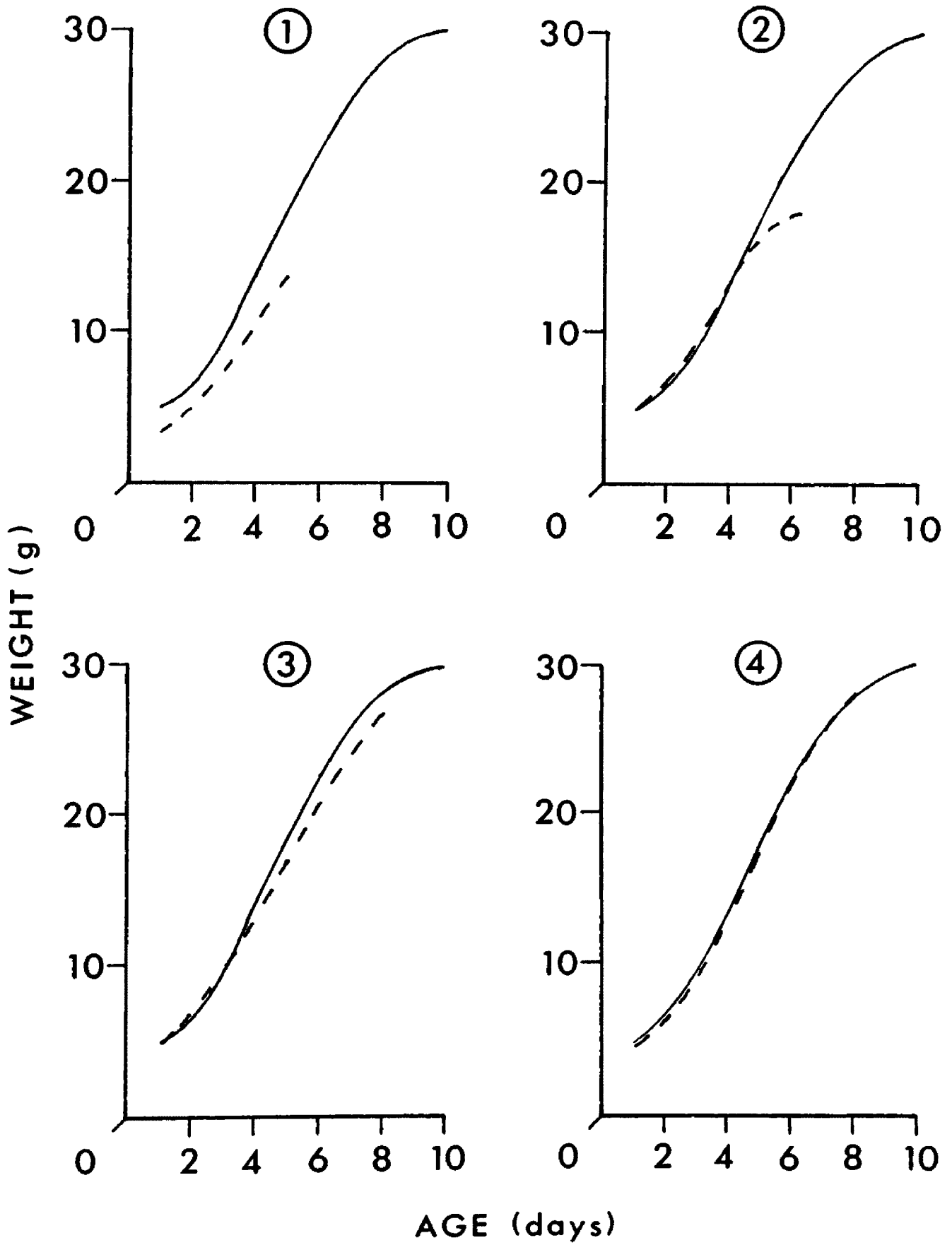
Starvation played a minor role in the mortality of solitaire nestlings during the two years of this study. In only two nests did possible starvation occur (83/6, and 84/3). Nest 83/6 was a cowbird-parasitized nest in which one nestling grew more slowly than the others and disappeared when eight days old. This nestling was presumably malnourished because of competition from the cowbird nestling. Nest 84/3 started out with five eggs, all of which hatched, but four of the five nestlings eventually died. The first one died when six days old, the next at eight days, and two died when nine days old. One of the latter was still in the nest, but the rest had disappeared without a trace. I doubt that an adult solitaire weighing 35-40g could carry off a dead nestling weighing about 25g but that may be what happened. Figure 14 compares the growth curves of the four nestlings which died with the one that survived to fledge. It can be seen that number 1 was lighter from the start, while 2 and 3 grew normally until shortly before they died, when they started to grow more slowly. Number 4 grew normally until it disappeared. As mentioned previously one nestling was found dead in the nest. This bird was collected, frozen upon return to campus, and given to Dr. B. O'Gara for autopsy. He

ascertained that the nestling died of pneumonia, but that it also had virtually no fat deposits. He concluded that the nestling died of pneumonia caused by being malnourished. The observed growth curves do not fit very well with this explanation that the nestlings died of starvation. One would expect a larger difference in growth rates between surviving and dying nestlings, if they did starve.

Only two of the 88 eggs laid failed to hatch. One of these was of normal size while the other (from nest 84/11) was only 67% of the average volume for solitaire eggs. This aberrantly small egg was 20% smaller than the next smallest egg; it is not surprising that it failed to hatch. This egg was in a nest that also had a cowbird egg present. It may be that the stress of being parasitized caused the female to lay such a small egg. As mentioned above, this nest (84/11) was abandoned shortly after the young hatched.

Of the final category of mortality ('other'), some losses did not fit into the earlier categories, and some causes were unknown. Two eggs from one nest (84/13) were destroyed during egg laying. When I checked the nest on the third day of egg laying one egg was in pieces on the bank below the nest. The second was in the nest and had a hole in it. When checked two hours later the nest was empty but the female was sitting on the nest! Shortly thereafter she laid her third egg, and a fourth the next day, both of which hatched and fledged. There are three possible explanations for this that I can imagine, none of which are very satisfactory. First, the eggs may have been preyed upon. It seems

Figure 14. Comparison of growth curve of surviving nestling from nest 84/3 with those of siblings.



unlikely that the female would return to the nest and continue laying if the nest had been found by a predator. Second, the eggs may have been destroyed by a female cowbird which never returned to lay her own egg. Cowbirds do not generally destroy all host eggs before laying their own, they do not usually leave egg fragments in the nest, and do not often destroy eggs without laying one of their own (Friedman 1963). It does not seem likely to me that a female solitaire would keep using a nest in which both eggs had been destroyed by any other organism. The third explanation is that the female solitaire deliberately destroyed her own eggs. Reasons for this might be that she somehowthesis.txt the eggs would not hatch and therefore removed them, or knew that food supplies were not sufficient to raise four young so she destroyed the first (and smallest) two eggs. In conjunction with this hypothesis see the discussion of nest 84/14 below. Again it is hard to explain the presence of shell fragments below the nest. Fragments were never found near nests where young successfully hatched. All shell fragments must have either been eaten by the adults or carried off. It is possible that the female solitaire (or cowbird) tried to carry off the egg but dropped it by mistake.

In nest 84/14 the female laid and started to incubate three eggs. One day before they were due to hatch one egg disappeared completely. On hatching day a second egg was found cracked on the bank below the nest. The third, and largest, egg hatched that day and the nestling survived to fledge, although it had ectoparasites and grew quite slowly (see Sec.VII). There are two explanations, and again, neither are very

satisfactory. First, a female cowbird may have found the nest and prepared to parasitize it but never did. It would not make sense for a cowbird to parasitize a nest after incubation has started because the egg would not have a good chance of being incubated sufficiently to hatch. Also the female solitaire is on the nest almost continuously during incubation so a cowbird would not have much opportunity to approach the nest. The second explanation is that the female solitaire destroyed the eggs intentionally. In both nests 84/13 and 84/14 the smallest eggs were the ones destroyed, which adds some support to this hypothesis. Also, both of these nests were initiated very late in the season (two or more weeks later than any others in 1984). This lends support to the idea that they were intentionally destroyed either because food was not sufficient or time was not available to raise a full clutch. There is no support for this hypothesis from the literature, as far as I can find.

Of the other miscellaneous losses of eggs and young one nest was destroyed by rocks falling in it (83/10) and one was destroyed by a road crew when they were widening the logging road (83/11). Two nestlings from two nests died after falling out of the nest. One of these nests was later lost to a predator (83/7) and the other abandoned (83/11) as discussed above.

The high nestling mortality during this study may be related either to my disturbances or to the fact that solitaires nest on the ground. Previous studies investigating the influence of observer visitation have found little (Willis 1973) or no (Nichols et al. 1984) influence of

human disturbance on nesting success. During the above studies, eggs and nestlings were not handled, so the disturbance was less severe than in the present study. Also, since I often had to climb the bank to inspect nests an obvious trail sometimes developed. Because of these factors it is probable that my activities had an adverse impact on nest survival, the magnitude of which is unknown. On the other hand, human activity in general was quite heavy on my study areas. It is uncertain whether predators could use my trails preferentially to find nests amid the numerous additional human trails present. Because nests were very widely dispersed it is unlikely that an individual predator learned to follow me or my tracks to active nests.

Ground nesting birds in general have been found to have higher mortality rates than tree-nesters (Ricklefs 1969b). Ricklefs calculated "instantaneous" daily mortality rates using the equation; $m = -(\ln P)/t$, where:

m = daily mortality rate.

P = proportion of eggs laid surviving to fledge.

t = length of nesting cycle (days).

Using this formula the Townsend's Solitaire has a daily mortality rate of 4.5%. This compares with mean mortality rates for five species of ground nesting birds of 3.7% and nine species of bush and tree nesters of 2.1%. Hole nesting species (7) had an even lower mortality rate of only 1.0% per day. It can be seen that ground nesters in general suffer high rates of mortality and that solitaire mortality is high even for ground nesters. If one assumes that solitaire mortality rates under

undisturbed conditions are similar to other ground nesters, then about 20% of the total solitaire mortality is due to human disturbance, my activities in particular. Under this scenario 31 (versus 25) of the eggs laid would have survived to fledge had I not been present. This is still only an average of 1.3 young fledged per active nest, compared with 1.1 for the present study.

SUMMARY

The Townsend's Solitaire is a migratory passerine species that can be found in parts of the western U.S., and in particular western Montana, throughout the year. Although solitaires' winter behavior is fairly well documented, very little information about its breeding biology has been published.

I found the Townsend's Solitaire to be fairly typical of small open-nesting passerines in its breeding biology. The major environmental factor influencing the evolution of reproduction and development in solitaires may be the high mortality rates associated with ground nesting. Mortality, and predation in particular, has been found to be higher for ground-nesting birds than for bush and tree-nesters. Solitaire mortality is high even for a ground-nesting bird, but this may be related to my activities around the nest.

Nests located during this study were generally situated on north-facing cutbanks where there was an overhang of at least 15cm. The female solitaire appears to build the nest and incubate the eggs without aid from the male, although he does seem to be involved in selecting a nest site. The observed egg laying rate of one egg/day, and incubation period of 12-13 days are typical of similar sized passerines. The solitaire patterns of increasing egg size with laying sequence, and

starting incubation after the last egg is laid also appear to be the norm for small open-nesting passerines exposed to high predation pressure.

Nestling solitaires are typically altricial, helpless and nearly naked when hatched. A nestling development rate of 0.53, and nestling period of 11-14 days again are fairly typical of open-nesting passerines in the same size range. The development rate of nestling solitaires is marginally faster than tree-nesters, but not faster than other ground-nesters. Solitaires fledge at about 33g, or 88% of adult body weight. The relatively rapid development and light fledging weight of the nestlings may be adaptations to minimize the length of the nestling period because predation rates are so high.

The majority of overall mortality occurred during the nestling period, primarily due to predation. A relatively high proportion of the mortality occurred during egg laying, considering that this period lasts only three days. This mortality was caused primarily by predators and Brown-headed Cowbirds. In contrast, nests during the incubation period suffered relatively low mortality. The period immediately after fledging may also be a time of high mortality (see Ricklefs 1969b for a discussion) although I lack data on this.

Brown-headed Cowbird parasitism was observed in 3 of 23 solitaire nests (13%) over two years. A study on Western Flycatchers (Empidonax difficilis) in the same area as the present study (Harper's Bridge area) in 1981 revealed that 5 of 12 flycatcher nests (42%) contained a single

cowbird egg (Dolan and Wright 1984). Western Flycatchers nest on cutbanks as solitaires do, but their nests are smaller and less conspicuous. This difference may be due to the fact that Townsend's Solitaire nests are uncommon and widely dispersed, relative to the Western Flycatcher's.

Two of 55 nestlings (4%) were observed to have dipteran larval ectoparasites of the genus Protocalliphora. This is a fairly common parasite of nestling passerines, and has been observed in western Montana previously (Pletch 1948, Jellison and Philip 1933). This ectoparasite appeared to slow the growth of one nestling, while the other was unaffected.

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APPENDIX I

83/1 Found: 5/29/83, complete but empty.

Location: Rock Cr. Rd., 0.1 mi. west of S. Side Rd.

Number of eggs laid: 4.

Egg laying dates: 6/1-6/5.

Number of eggs hatched: ????

Hatching date: 6/17.

Number of young fledged: 0.

Fledging dates: N/A.

Incubation period: 12 days.

Nestling period: N/A.

Fate: Nest destroyed by unknown predator 6/17 or 6/18.

83/2

Found: 5/29/83, contained 4 eggs.

Location: Rock Cr. Rd., 0.2 mi. west of S. Side Rd.

Number of eggs laid: 4(?).

Egg laying dates: unknown.

Number of eggs hatched: 4.

Hatching date: 5/30.

Number of young fledged: 4.

Fledging date: 6/10.

Incubation period: unknown.

Nestling period: 11 days.

Fate: Fledged four young.

83/3

Found: 5/29/83, empty.

Location: S.Side Rd., approx. 100m. east of Rock Cr. Rd.

Number of eggs laid: 4.

Egg laying dates: 6/7-6/10.

Number of eggs hatched: 4.

Hatching date: 6/22.

Number of young fledged: 4.

Fledging date: 7/5.

Incubation period: 13 days.

Nestling period: 12 days.

Fate: Fledged four young.

83/4

Found: 6/1/83

Location: S. Side Rd., 2 miles south of Harper's Bridge.

Number of eggs laid: 2.

Egg laying dates: 6/1-6/2.

Number of eggs hatched: N/A.

Hatching date: N/A.

Number of young fledged: N/A.

Fledging dates: N/A.

Incubation period: N/A.

Nestling period: N/A.

Fate: Destroyed by unknown predator on 6/2 with two eggs in nest.

83/5

Found: 6/1/83, with dirt and pebbles in it.

Location: Albert Cr. Rd., approx. 0.3 mi. west of S. Side Rd.

Number of eggs laid: N/A.

Egg laying dates: N/A.

Number of eggs hatched: N/A.

Hatching dates: N/A.

Number of young fledged: N/A.

Fledging dates: N/A.

Incubation period: N/A.

Nestling period: N/A.

Fate: Old nest, never used.

83/6

Found: 6/4/83, partially complete.

Location: Junction of Albert Cr. Rd. and S. Side Rd.

Number of eggs laid: 5 (plus 1 cowbird).

Egg laying dates: 6/18-6/22

Number of eggs hatched: 1 cowbird).

Hatching dates: 7/5.

Number of young fledged: 1 (plus 1 cowbird).

Fledging dates: 7/15-7/16.

Incubation period: 13 days.

Nestling period: 10-11 days.

Fate: Fledged one solitaire and one cowbird.

83/7

Found: 6/2/83, with four nestlings present.

Location: Sherman Gulch Rd., approx. 0.2 mi. west of S. Side Rd.

Number of eggs laid: unknown.

Egg laying dates: unknown.

Number of eggs hatched: .

Hatching date: 5/31 or 6/1.

Number of young fledged: 0.

Fledging dates: N/A.

Incubation period: unknown.

Nestling period: N/A.

Fate: One nestling fell from nest 6/7, nest predated on 6/8.

83/8

Found: 6/2/83, with four eggs present.

Location: S. Side Rd., approx. 0.2 mi. north of Rock Cr. Rd.

Number of eggs laid: 4 (?).

Egg laying dates: unknown.

Number of eggs hatched: 4.

Hatching date: 6/3.

Number of young fledged: 4.

Fledging date: 6/16.

Incubation period: unknown.

Nestling period: 12 days.

Fate: Fledged four young.

83/9

Found: 6/2/83, with three eggs present.

Location: S. Side Rd. approx. 0.8 mi. south of Albert Cr. Rd.

Number of eggs laid: 3 (?).

Egg laying dates: unknown.

Number of eggs hatched: 0.

Hatching dates: N/A.

Number of young fledged: 0.

Fledging dates: N/A.

Incubation period: N/A.

Nestling period: N/A.

Fate: abandoned on 6/10.

83/10

Found: 6/27/83, with one egg present.

Location: S. Side Rd. Approx. 100m. south of Albert Cr. Rd.

Number of eggs laid: 4 (?).

Egg laying dates: 6/27(?) - 6/30.

Number of eggs hatched: 0.

Hatching dates: N/A.

Number of young fledged: 0.

Fledging dates: N/A.

Incubation period: N/A.

Nestling period: N/A.

Fate: destroyed by rocks falling in nest, precise date unknown.

83/11

Found: 6/3/83, with four eggs present.

Location: Bonner, MT.

Number of eggs laid: 4 (?).

Egg laying dates: unknown.

Number of eggs hatched: 4.

Hatching date: 6/13.

Number of young fledged: 0.

Fledging dates: N/A.

Incubation period: unknown.

Nestling period: N/A.

Fate: Cutbank containing nest blown up by road crew widening road.

84/1

Found: 5/19/84, complete but empty.

Location: Rock Cr. Rd. 0.2 mi. west of S. Side Rd. (10m. west of nest 83/2).

Number of eggs laid: 4.

Egg laying dates: 5/24-5/27.

Number of eggs hatched: 4.

Hatching date: 6/9.

Number of young fledged: 4.

Fledging date: 6/21.

Incubation period: 13 days.

Nestling period: 12 days.

Fate: Fledged four young.

84/2

Found: 5/23/84, partially complete.

Location: S. Side Rd. approx. 0.15 mi. south of Cyr Gulch Rd.

Number of eggs laid: 5.

Egg laying dates: 5/31-6/4.

Number of eggs hatched: 0.

Hatching dates: N/A.

Number of young fledged: 0.

Fledging dates: N/A.

Incubation period: N/A.

Nestling period: N/A.

Fate: nest abandoned on 6/9.

84/3

Found: 5/26/84, complete but empty.

Location: S. Side Rd. approx. 1 mi. south of Albert Cr. Rd

Number of eggs laid: 5.

Egg laying dates: 5/30-6/4.

Number of eggs hatched: 5.

Hatching date: 6/15.

Number of young fledged: 1.

Fledging date: 6/25.

Incubation period: 11 days.

Nestling period: 10 days.

Fate: One nestling fledged, the rest died in the nest, presumably of starvation.

84/4 Found: 5/24/84, nest foundation started.

**Location: Sherman Gulch Rd. approx. 0.15 mi. west of S. Side Rd.
(at site of nest 83/7).**

Number of eggs laid: 4.

Egg laying dates: 6/2-6/5.

Number of eggs hatched: 0.

Hatching dates: N/A.

Number of young fledged: 0.

Fledging dates: N/A.

Incubation period: N/A.

Nestling period: N/A.

**Fate: nest destroyed and eggs predated by unknown predator on
6/6-6/7.**

84/5 Found: 6/1/84, complete but empty.

Location: Pattee Canyon (see Fig. 3).

Number of eggs laid: 4.

Egg laying dates: 6/3-6/6.

Number of eggs hatched: 0.

Hatching date: N/A.

Number of young fledged: 0.

Fledging dates: N/A.

Incubation period: N/A.

Nestling period: N/A.

**Fate: nest destroyed and eggs predated by unknown predator on
6/19-6/20.**

84/6

Found: 6/1/84, almost complete.

Location: Pattee Canyon (see Fig. 3).

Number of eggs laid: 4.

Egg laying dates: 6/3-6/6.

Number of eggs hatched: 4.

Hatching date: 6/19.

Number of young fledged: 4.

Fledging dates: 7/2-7/3.

Incubation period: 13 days.

Nestling period: 13-14 days.

Fate: Fledged four young.

84/7

Found: 5/27/84, complete but empty.

Location: Pattee Canyon (see Fig. 3).

Number of eggs laid: unknown.

Egg laying dates: unknown.

Number of eggs hatched: 0.

Hatching dates: N/A.

Number of young fledged: 0.

Fledging dates: N/A.

Incubation period: N/A.

Nestling period: N/A.

Fate: Nest destroyed before or soon after first egg laid.

84/8 Found: 6/1/84, complete but empty.

Location: Pattee Canyon (see Fig. 3).

Number of eggs laid: 4.

Egg laying dates: 6/2-6/5.

Number of eggs hatched: 3.

Hatching date: 6/17.

Number of young fledged: 0.

Fledging dates: N/A.

Incubation period: 12 days.

Nestling period: N/A.

Fate: One egg infertile, three nestlings predated on 6/26 when nine days old by a buteo, probably a Red-tailed Hawk (Buteo jamaicensis).

84/9 Found: 5/23/84, partially complete.

Location: S. Side Rd. approx. 0.4 mi. south of Rock Cr. Rd.

Number of eggs laid: 4 (plus 1 cowbird).

Egg laying dates: 6/11-6/14

Number of eggs hatched: 1 (plus 1 cowbird).

Hatching date: 6/26.

Number of young fledged: 0.

Fledging date: N/A.

Incubation period: 12 days.

Nestling period: N/A.

Fate: Parasitized by cowbird, one solitaire egg survived to hatch, nestlings predated by unknown predator on 6/30.

84/10 Found: 6/9/84, nest almost complete.

Location: Junction of Albert Cr Rd. and S. Side Rd. (same as 83/6).

Number of eggs laid: 2.

Egg laying dates: 6/11-6/12

Number of eggs hatched: 0.

Hatching dates: N/A.

Number of young fledged: 0.

Fledging dates: N/A.

Incubation period: N/A.

Nestling period: N/A.

Fate: Eggs predated after second egg laid.

84/11

Found: 6/14/84, containing four eggs (including one cowbird egg).

Location: Blue Mtn. Rd., by entrance to recreation area.

Number of eggs laid: 3 (?).

Egg laying dates: unknown.

Number of eggs hatched: 2 (plus 1 cowbird).

Hatching dates: 6/20-6/21.

Number of young fledged: 0.

Fledging dates: N/A.

Incubation period: unknown.

Nestling period: N/A.

Fate: Cowbird-parasitized, two solitaires and one cowbird hatched, nest abandoned on 6/22.

84/12

Found: 6/16/84, with three eggs present.

Location: S. Side Rd. approx. 0.5 mi. south of Harper's Bridge.

Number of eggs laid: 4.

Egg laying dates: 6/14(?) - 6/18.

Number of eggs hatched: 4.

Hatching date: 6/30.

Number of young fledged: 0.

Fledging date: N/A.

Incubation period: 12 days.

Nestling period: N/A.

Fate: Nestlings predated on 7/2 by an avian predator.

84/13

Found: 6/23/84, with foundation complete.

Location: Rock Cr. Rd. approx. 1.25 mi. west of S. Side Rd.

Number of eggs laid: 4.

Egg laying dates: 6/24 - 6/28.

Number of eggs hatched: 2.

Hatching date: 7/10

Number of young fledged: 2.

Fledging date: 7/23.

Incubation period: 12 days.

Nestling period: 13 days.

Fate: Two eggs destroyed during egg laying, two young fledged.

84/14 Found: 6/24/84, with foundation complete.

Location: approx. 0.08mi. up logging road off Rock Cr. Rd. approx.
1.5 mi. west of S. Side Rd.

Number of eggs laid: 3.

Egg laying dates: 6/28-7/1.

Number of eggs hatched: 1.

Hatching date: 7/12.

Number of young fledged: 1.

Fledging date: 7/26.

Incubation period: 11 days.

Nestling period: 14 days.

Fate: One egg disappeared on 7/11, one egg found destroyed on bank
below nest on 7/12, one young fledged.

84/15

Found: 7/12/84, foundation just started.

Location: S. Side Rd. approx. 0.1 mi. south of Rock Cr. Rd.

Number of eggs laid: 0.

Egg laying dates: N/A.

Number of eggs hatched: 0.

Hatching dates: N/A.

Number of young fledged: 0.

Fledging dates: N/A.

Incubation period: N/A.

Nestling period: N/A.

Fate: Nest never completed or used.