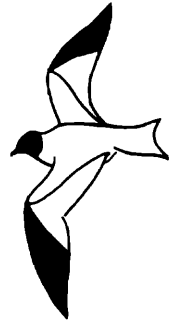


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CLUTCH SIZES AND NESTING HABITS OF BIRDS AT TIOGA PASS

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ABSTRACT: We recorded clutch sizes for several birds, mostly passerines, during a lengthy study of vertebrate populations in the Sierra Nevada of California near Tioga Pass. Here we report frequencies of the various clutch sizes observed, descriptions of nest sites, and other natural-history notes. In at least three species, the Hermit Thrush (*Catharus guttatus*), American Robin (*Turdus migratorius*), and White-crowned Sparrow (*Zonotrichia leucophrys*), clutches in this montane setting tended to be larger than those reported for lowland regions. In the two species studied in greatest detail, the Dusky Flycatcher (*Empidonax oberholseri*) and White-crowned Sparrow, clutch size decreased through the breeding season with date of clutch initiation. We suggest that this commonly observed seasonal trend is cued by decreasing day length and that it is an expression of a gradual, as opposed to abrupt, onset of photorefractoriness.

Clutch size is probably the most commonly evaluated of all life-history traits in studies of avian reproduction. It is easily obtained and provides a measure of function that is broadly applicable to comparisons within and among species (Stearns 1992, Roff 2002). Furthermore, clutch size, along with the date of clutch initiation, is useful for understanding investment strategies of seasonal breeders that have broad geographic ranges.

METHODS

The study site was in Mono County, California, in the Sierra Nevada. Over three decades, 1968–1997, we studied vertebrate populations in the vicinity of Tioga Pass, at about 3000 m altitude, in the upper branches of Lee Vining Canyon from Ellery Lake to the Yosemite National Park boundary, including about 2 km each along Mine Creek and Lee Vining Creek. During these studies, we accumulated data on clutch sizes and other aspects of natural history, such as nesting sites, on various birds. We determined a clutch's starting date by at least one visit during the laying period (assuming that one egg was laid per day) and clutch size by at least two visits following the completion of laying.

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Table 1 Frequency of Clutch Sizes of 15 Species at Tioga Pass

Species	n	Clutch size								Mean	SD ^b
		2	3	4	5	6	7	8			
Mallard (<i>Anas platyrhynchos</i>)	3	0	0	0	0	0	1	2	7.67	0.58	
Spotted Sandpiper (<i>Actitis macularius</i>)	30	0	4	26	0	0	0	0	3.87	0.34	
Dusky Flycatcher (<i>Empidonax oberholseri</i>)	111	6	35	70	0	0	0	0	3.58	0.60	
Mountain Chickadee (<i>Poecile gambeli</i>)	10	0	0	0	0	6	2	2	6.60	0.84	
Rock Wren (<i>Salpinctes obsoletus</i>)	10	0	0	1	3	5	1	0	5.60	0.84	
Mountain Bluebird (<i>Sialia currucoides</i>)	3	0	0	0	1	2	0	0	5.67	0.58	
Hermit Thrush (<i>Catharus guttatus</i>)	92	1	16	74	1	0	0	0	3.82	0.44	
American Robin (<i>Turdus migratorius</i>)	30	0	8	22	0	0	0	0	3.73	0.45	
Yellow-rumped Warbler (<i>Dendroica coronata</i>)	7	0	1	4	2	0	0	0	4.14	0.69	
Wilson's Warbler (<i>Wilsonia pusilla</i>)	3	0	1	1	1	0	0	0	4.00	1.00	
Song Sparrow (<i>Melospiza melodia</i>)	7	0	0	5	2	0	0	0	4.29	0.49	
Lincoln's Sparrow (<i>Melospiza lincolni</i>)	5	0	1	2	2	0	0	0	4.20	0.84	
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>) ^a	1154	14	196	878	64	2	0	0	3.86	0.51	
Dark-eyed Junco (<i>Junco hyemalis</i>)	112	0	11	98	3	0	0	0	3.93	0.35	
Brewer's Blackbird (<i>Euphagus cyanocephalus</i>)	14	0	0	9	5	0	0	0	4.36	0.50	

^aData from Morton (2002).

^bSD, standard deviation.

RESULTS AND DISCUSSION

We found three or more clutches of 15 species, all passerines except the Mallard (*Anas platyrhynchos*) and Spotted Sandpiper (*Actitis macularius*) (Table 1). Nearly all clutches were started between late May and mid-July.

Mallard

Mallard nests were located in marshy areas in subalpine meadows, and the first one found was at the highest altitude (3002 m) recorded for this species' breeding in California (Morton and Morton 1973). Eventually, we discovered two additional nests, and one of them hatched all eggs. On 25 July 1993 we observed the female leading the ducklings from this nest and into a patch of willows (*Salix* spp.) The next day they were swimming on a small tarn about 200 m from the nest location.

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Spotted Sandpiper

The modal clutch size of the Spotted Sandpiper over a wide range of longitudes is four, with three eggs sometimes being laid late in the season. Either sex may choose the nest site, and a strong preference for previously used sites is based on experience (Oring et al. 1997). Our Tioga Pass data are in agreement with these generalizations (Table 1). Nests on our study area were built on sand bars, on small islands within creeks, and in marshy spots at the margins of lakes or tarns. Site preferences were evident in that nests were sometimes placed in precisely the same location in up to three consecutive years. One of these, for example, was in a shallow depression under a small willow (20–40 cm high) or lodgepole pine (*Pinus contorta*).

In one notable nesting cycle the first egg was laid on 28 June just as a storm commenced and buried the nest in snow. Laying resumed in this same nest, then snow free, on 5 July. On 20 July we flushed the incubating adult from four eggs, and on 27 July one egg was missing and one pipped egg and two chicks remained. Three chicks departed the nest early the next morning.

Dusky Flycatcher

From 1981 to 1985, during a study focused primarily on regulation of egg temperatures and developmental processes in nestlings (Morton and Pereyra 1985, Pereyra and Morton 2001), we recorded data on clutch initiation and clutch size of the Dusky Flycatcher. A few of the 111 nests were in meadows, these usually in willows, but most were at the periphery of meadows in lodgepole pines, willows, or stunted aspens (*Populus tremuloides*), often on talus-covered slopes. Clutches ranged in size from two to four (Table 1), with four being the mode. Four-egg clutches are particularly common in this species in first nests of the season (Sedgwick 1993).

Rock Wren

We noted clutch sizes of Rock Wrens (*Salpinctes obsoletus*) during a study of their incubation behavior and its effects on egg temperature. Their nests were usually located on talus slopes and were built in cavities under rocks or within rocky outcrops (Oppenheimer and Morton 2000).

Mountain Chickadee and Mountain Bluebird

Both the Mountain Chickadee (*Poecile gambeli*) and Mountain Bluebird (*Sialia currucoides*) are hole nesters, but the only clutches for which we obtained reliable data were laid in nest boxes (all listed in Table 1). Presumably they are representative of those laid in natural cavities.

Hermit Thrush

Across its range, the Hermit Thrush varies considerably in its choice of nest site. East of the Rocky Mountains the majority build on or near the ground, whereas west of the mountains nests tend to be higher (Jones and Donovan 1996). In central Arizona, for example, Martin and Roper (1988) found nests in small white firs (*Abies concolor*) almost exclusively, at a mean height of 1.1 m. Habitat features influencing nest-site selection at Tioga Pass

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appeared to be much the same as those in Arizona. Of the 92 nests noted in Table 1, five were in willows, one was in a white-barked pine (*P. albicaulis*), and 86 were in lodgepole pines. Most of these pines were young and no more than 2–3 m tall. Mean nest height was 1.0 m (standard deviation 0.5 m, range 0.2–2.7 m).

The mode of Hermit Thrush clutch size is four eggs, but means tend to be larger in the west (Jones and Donovan 1996). The mean clutch at Tioga Pass of 3.82 eggs is actually significantly larger than the mean of 3.56 noted by Jones and Donovan (1996) for other western populations ($P < 0.05$). Perhaps birds in general lay clutches at high elevations larger than expected from longitudinal or latitudinal trends in the same species at low elevations, as shown previously in the White-crowned Sparrow (Morton 1976).

American Robin

In spring American Robins tend to move upward behind the melting snowline in the Sierra Nevada, a pattern especially noticeable on the more gradual western slope, and they are among the earliest of the migratory passerines to arrive and to begin nesting around Tioga Pass (DeSante 1990). Egg laying sometimes began as early as the latter half of May. All the nests we found were in lodgepole pines. The 30 clutches noted in Table 1 were accessible from the ground or by a short climb; we did not try to climb to nests located high up in the taller trees.

All clutches were of either three or four eggs; the mean was 3.73. This figure is larger than that reported from most other locations across North America (Sallabanks and James 1999). Although at 30 our sample size was small, this difference suggests that the robin's clutch size increases with elevation, as for the Hermit Thrush.

We did not visit most robin nests regularly, but it is our impression that they seldom experienced predation. Robins are well known to mob and attack potential predators, and these behaviors may be highly effective. Although Sallabanks and James (1999) mentioned many predators on robin nests, including several corvids, Clark's Nutcracker (*Nucifraga columbiana*) was not among them. We note, therefore, that at one American Robin nest a Clark's Nutcracker succeeded in removing two of the four eggs despite vigorous defense by the parents. At another time and location we observed a robin successfully drive off a nutcracker that was flying by the nest tree. It accosted the nutcracker in mid-air, then grabbed a wing with its beak and yanked vigorously until the nutcracker managed to pull away.

Yellow-rumped Warbler and Wilson's Warbler

Although warblers were around Tioga Pass every year, we made no special effort to find their nests so obtained data on only a few. All of the seven Yellow-rumped Warbler (*Dendroica coronata*) nests were in small lodgepole pines, and the three Wilson's Warbler (*Wilsonia pusilla*) nests were on the ground beneath large willows. Stewart et al. (1978) conducted a multi-year study of Wilson's Warbler breeding biology on the eastern edge of our study area.

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Song Sparrow and Lincoln's Sparrow

A few Song Sparrows (*Melospiza melodia*) and Lincoln's Sparrows (*M. lincolni*) nested most years within our focal study area. Song Sparrow nests were built on the ground or just above it in thick willows. All the Lincoln's Sparrow nests we discovered were on the ground. In the meadows near Tioga Pass both of these species were greatly outnumbered by White-crowned Sparrows. Although smaller, they sometimes prevailed in agonistic encounters with the White-crowned. In a few cases they even caused White-crowns to abandon nests near their own. A Brown-headed Cowbird (*Molothrus ater*) egg was with four Song Sparrow eggs in one nest, and three sparrows and the cowbird fledged from it. This was the only example of cowbird fledging that we observed at any time in the study.

White-crowned Sparrow

The migratory montane subspecies of the White-crowned Sparrow, *Z. l. oriantha*, is the most abundant passerine in the subalpine meadows of the Tioga Pass area and was the primary focus of our studies. Thus we recorded extensive data on its nesting habits, including clutch size (Table 1). Many of these data, including those on nest-site selection, were addressed at length by Morton (2002), so we mention only a few points here. Clutches of the modal size, four, were not as productive as those of five eggs; that is, more young tended to be fledged from the larger clutches (neither of the two six-egg clutches survived). If their nest failed, the birds laid a replacement clutch, sometimes repeatedly, all through June and July. Also, Morton et al. (2004) found a cost of reproduction, as expressed in quality of young and in survival of adults, in relation to reproductive effort. Finally, clutch size decreased significantly through the breeding season (see below).

Dark-eyed Junco

Junco nests were built on the ground and were usually well hidden beneath a clump of grass that provided a screening overhang. We found a few interesting deviations from this pattern, however. For example, one nest was built into the end of a fallen log, another was among the still-green needles of a fallen lodgepole pine, another was in a hole in a muddy bank, and another was simply placed in the open amid the fallen needles of a Jeffrey pine (*P. jeffreyi*).

The modal clutch size of the Dark-eyed Junco is usually four (Austin 1968), the same as we found (Table 1). Although five-egg clutches are rare at Tioga Pass, in northern Utah Smith and Andersen (1985) found their frequency to increase in years of late snowmelt. These authors suggested that an extra egg might have been laid because females were able to accumulate reserves while waiting for nesting sites to clear. At our study site juncos may not have been delayed appreciably in years of heavy snow because they often nest on steep south-facing slopes, among the first places to become free of snow.

Brewer's Blackbird

During the first 20 years of the study we observed this species but usually only from mid-summer onward, when flocks flew in and foraged on the

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meadows, especially in the morning. We presumed that these birds were from breeding colonies in the shrub-steppe at the lower end of Lee Vining Canyon near Mono Lake, some 10–20 km away. Then, in June 1987, Brewer's Blackbirds began nesting in our study area and have continued to do so every year since. One of their nests was built on the ground amid low willows; the rest were in lodgepoles. In the last few years they have tended to concentrate around Tioga Pass Resort and nearby campgrounds, where they sometimes feed on scraps discarded by motorists and campers. Why Brewer's Blackbirds suddenly colonized Tioga Pass in 1987 is uncertain, but it may have been because the area has gradually become drier. Additional evidence for this hypothesis is that Brewer's Sparrows (*Spizella breweri*), which ordinarily nest in dry habitats at lower elevations of the eastern Sierra, also became more noticeable in the small, scattered patches of sagebrush (*Artemisia tridentata*) high up on the south- and east-facing slopes of the study area. Simultaneously, the once robust breeding population of the Yosemite toad (*Bufo canorus*) died out, probably in part because of the disappearance of marshy areas and the silting in of small tarns suitable for egg laying (Sherman and Morton 1993). Also, lodgepole pine seedlings began to invade more deeply into the meadows. We do not know if these alterations in community structure reflect regional or global climatic fluctuations, but changes in breeding distribution, such as that of Brewer's Blackbird, may prove to be useful biotic indicators of such phenomena.

Other Species

During our study we verified one complete clutch each of the following species: White-breasted Nuthatch (*Sitta carolinensis*), five eggs; Townsend's Solitaire (*Myadestes townsendi*), four eggs; Chipping Sparrow (*Spizella passerina*), four eggs; and Red-winged Blackbird (*Agelaius phoeniceus*), six eggs. A pair of Red-wings nested in a marshy area in June 1990 and hatched nestlings that were lost to a predator. The following year a pair in another marsh about 600 m away probably had a nest but then disappeared, apparently without fledging young. These were the only times we observed Red-winged Blackbirds in the study area.

Seasonal Changes in Clutch Size

A downward trend in clutch size through the reproductive season has been observed in many species of birds (Klomp 1970), but an unambiguous demonstration of this decrease is not always a simple matter: nests have to be found in sufficient quantity throughout the breeding season, first egg dates should be known so as to fix the chronology accurately, and clutch size must be variable. For example, a seasonal decrease in clutch size has been demonstrated in the Dark-eyed Junco (Smith and Andersen 1982), but our data on that species were unsuitable for detecting this result because we seldom knew exactly when eggs were laid and most clutches (87.5%) were of four eggs. On the other hand, we had gathered information on Dusky Flycatchers and White-crowned Sparrows more carefully, and clutch size decreased in both of them (Figure 1).

In the ultimate sense, such a decrease in parental investment could be an important strategy if food appropriate for rearing young, such as insect

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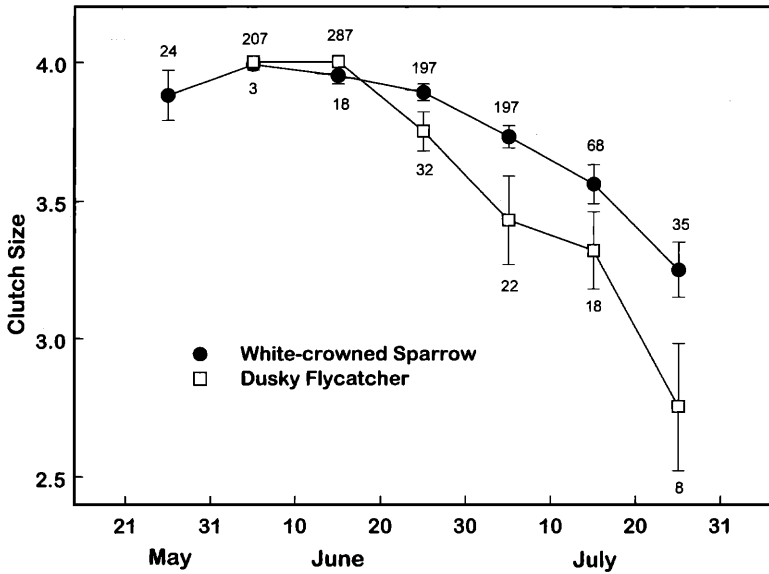


Figure 1. Mean clutch sizes (± 1 standard error) in the White-crowned Sparrow and Dusky Flycatcher in relation to clutch-initiation date (abscissa). Sample sizes are shown above the error bars for sparrows and below the bars for flycatchers.

larvae, dwindle in availability simultaneously. Food supply is not an effective proximate cue for inhibiting ovarian function, however, as shown clearly by food-supplementation studies and large annual variations in environmental conditions such as weather and residual snowpack that affect food availability strongly (Daan et al. 1988, Rowe et al. 1994, Morton 2002). Because calendar date is usually the best predictor of clutch size, the most likely cue for decreasing clutch size over time is decreasing day length (Murphy and Haukioja 1986). The birds lose their ability to lay completely when they become photorefractory, but the onset of this condition appears to be gradual rather than abrupt (Meijer et al. 1992). Thus seasonal decreases in clutch size may result from a mechanism that has evolved for the purpose of terminating reproduction at an appropriate time rather than from short-term feedback from environmental conditions such as food abundance. Hypotheses regarding control mechanisms aside, seasonal decreases in clutch size can be substantial (Figure 1). Recognition of this trend should be factored into assessments of parental effort and potential costs of reproduction in studies that rely heavily on clutch-size data. For quick comparisons of reproductive investment among populations, the currently most useful single indicator is probably the modal clutch size.

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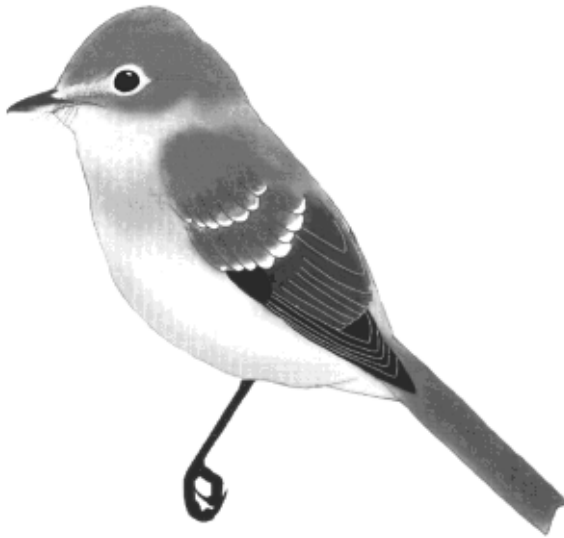
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Dusky Flycatcher

Sketch by George C. West, Birchside Studios