Nesting Adaptations of Tricolored Blackbirds
(*Agelaius tricolor*)

Final Draft

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INTRODUCTION

Over ninety five percent of California's seasonal marshes have been lost since the arrival of Europeans, and many avian species associated with these habitats have experienced population decline. Current conservation efforts to create or restore wetland habitat, including marshes, are almost entirely designed to enhance migrating and resident waterfowl populations. Very little attention has been given to the conservation of other avian groups associated with marshes, including numerous passerine species that use wetland habitats for breeding and foraging.

The tricolored blackbird (*Agelaius tricolor*: family *Icteridae*) is a highly colonial California endemic species which historically nested almost exclusively in deepwater marshes (Neff, 1937). Tricolored blackbirds are similar in appearance to redwinged blackbirds (*A. phoenicus*) and are probably close relatives (Orians, 1961). However, whereas the redwing has a continental distribution in North America, the tricolored blackbird's range is limited to California west of the Sierra Nevada and small portions of southernmost Oregon (Neff, 1937). Historic records also include colonies in northern Baja California, but none have been reported in recent years (Beedy *et al.*, 1991).

Tricolored blackbird colonies vary widely in size, ranging from less than ten breeding adults to as many as three hundred thousand, though colonies smaller than fifty are rare (Neff, 1937; Orians, 1961; Orians and Collier, 1963; DeHaven *et al.*, 1975; Bowen *et al.*, 1992; Hamilton, 1993). Tricolored blackbirds forage in upland habitats away from colonies, travelling six and a half kilometers or more to feeding grounds (Orians, 1961; Orians and Collier, 1965; Hamilton, pers. comm.; pers. obs.). Concentrations of insect prey within foraging distance of colonies are therefore necessary for colony success (Orians, 1961; Orians and Collier, 1963). The unpredictable annual distribution of tricolored blackbird colonies is likely due to adaptation to the instability of historic marsh nesting habitat driven by annual winter flooding, and also by patchy concentrations of insect prey (Orians, 1961). Since the 1930's, tricolored blackbirds have continually extended their choice of nesting habitat to include upland vegetation, involving various species of native and exotic thistles, wild rose and blackberries (Beedy *et al.*, 1991). During the five years of his study of tricolored blackbird distribution and habitat use in the early 1930's, Neff (1937) reported 235 of 242 (97%) of all the colonies he located to occur in marshes, primarily in dense cattail (*Typha* spp.) stands. Only three percent occurred at upland sites. By the early 1970's, a twenty five percent increase in upland habitat use had occurred (40 of 156 colonies observed between 1972 and 1975 were located in upland sites (DeHaven *et al.*, 1975)). By between 1.5 and 2.5 nestlings per nest surviving to eight days of age. Of the five upland colonies, three occurred in Himalaya berries. Mean nestling survivorship across these colonies were the highest measured anywhere (range = 2.0 to 2.5 nestlings per nest). Qualitative observations at nine other Himalaya berry sites during the study also indicated similarly high nesting success. Using the same methods, Hamilton, in 1993, found nestling survivorship in seven of nine cattail marshes to range from none to no more than 0.9 nestlings per nest, though survivorship in the remaining two colonies was higher (1.87 and 1.88) (Hamilton, 1993).

The low nesting success rates observed across marsh colonies were largely or entirely a result of whole clutch losses, for which the authors observed strong evidence implicating predation on nestlings. Whole clutch loss across Himalaya berry colonies at the same time were rare (7 of 113 (6%) of sampled nests). Partial clutch loss at all colonies observed in most cases appeared to be a consequence of starvation of one of more nestlings. Mean starvation rates did not appear to differ significantly between marsh and upland colonies: marsh colonies averaged 2.0 starved nestlings per nest compared to 2.3 across upland colonies. Differences in nesting success between marsh and upland habitats therefore appeared to be almost entirely a function of differential predation pressure.

This study provides evidence which shows that nesting adaptations of tricolored blackbirds to Himalaya berry habitat has been important to the species' survival, at least in recent years. The results are thus concluded to be highly significant to efforts to conserve tricolored blackbirds.

METHODS

Study Area

The study area consisted of a one thousand square kilometer portion of the southeastern corner of Sacramento County, located in north central California. Site decision was based on personal observations in 1991 and 1992, and reports in Beedy *et al.* (1991) of high colony density and between colony nesting synchrony in that part of the tricolored blackbird's breeding range. The site was bordered by Highways 99 to the west and 16 to the north, and by county boundaries to the east and south. Typical habitat for the region is flat Central Valley and lower foothill grassland. The study site contained numerous natural and manmade streams courses, cattle ponds and degraded vernal pools. Human settlement was rural but the site also extended to the southern limits of Sacramento city and the town of Galt. Land use was primarily livestock grazing and included numerous small ranches and two dairies. Much of the area however was in the process of conversion to multi-acre subdivisions, many of which during the previous two or more years had been left fallow or only lightly used.

Tricolored blackbird nesting habitat at the study site consisted primarily of large Himalaya blackberry thickets measuring approximately three meters to one kilometer in length and three to ten meters high (pers. obs.). Several small (less than four hectares) deepwater cattail marshes also occurred which had been used as breeding sites in years previous to and following this study (pers. obs.).

Sample Colonies

The study was conducted during the spring and early summer months of 1993. Weekly surveys of the site began on April 16th, and were discontinued on May 22nd when eleven potential sample colonies had been identified. The population of colonies sampled were all of those which were synchronized to within two weeks of each other and of which I was able to obtain access. Table 1 lists adult population sizes, substrate types and settlement dates of colonies sampled. Dates of settlement were derived by extrapolating back from the dates eggs first began hatching. Settlements occurred between April 25th and May 6th. Seven of the eight colonies included in this study were located in Himalaya berries. The remainder occurred in a four hectare cattail marsh.

Because increasing numbers of competitors (colony size in this case) may reduce resource availability (see Milinski and Parker, 1991), colony size was included as a sample variable. Colonies included in the study ranged from very small - thirty breeding adults, to large - fifteen thousand breeding adults.

Colony Size Estimates

The difficulty of estimating colony sizes was realized in the previous two years work with the species. Much effort in those years was devoted to developing ability to estimate colony sizes. Part of this effort included photographing flocks after estimating numbers of individuals in the field and later enumerating them from the photographs for comparison. A second effort included sampling nest densities after adults and young had dispersed from a colony site. Those data were then used to extrapolate an estimate of the total number of adults that had been present. The calculated colony size was finally compared to the earlier field count of adults at the colony. This method provided a means of calibrating field counts of adults at colonies and gauging the accuracy of those counts. During this study, colony sizes were estimated upon each visit to the colonies. However, because the adult population is most visible when provisioning young, final estimates were decided at that stage. Colony sizes were estimated following the procedures above, only qualitative estimates of nest densities were made. Reported colony sizes are believed to have been accurate to within 15%.

Biological Data

Two measures were used as indicators of reproductive success. One was nestling survivorship as measured by the actual number of offspring surviving to eight days after the first egg(s) began hatching. The second was an indicator of general nestling health as measured by nestling weight when nestlings were eight days of age. It was not practical to collect data from nestlings older than eight days because of the propensity of these to fledge prematurely when approached. Thus no attempt was made to follow nestling survivorship beyond eight days, and nests containing offspring older than eight days were avoided to prevent encouraging premature fledging.

Sample sizes of no more than twenty five nests per colony were decided upon in an effort to balance adequate sample size requirements while also minimizing disturbance to colonies. Transects were designed to capture every nest in a randomly chosen accessible section of the colony. To restrict the number of visits to colonies, it was necessary to include only nests which were well synchronized with respect to hatching. The sample population of nests therefore included those which contained at least one hatched offspring and offspring no more than two days old. Tricolored blackbird nestlings are easily aged by casual visual observation between one and eight days of age. Because previous years' observations (Bowen *et al.*, 1992) strongly indicated that partial clutches of eggs were rarely lost, this method also enabled data collection of clutch sizes to be postponed until after hatching was underway.

Once sample colonies were chosen, each was monitored for indications of signs of hatching. Tricolored blackbird nesting stages are discernable in the field once the gross behavior of colonies is understood (Hamilton, pers. comm.; pers. obs.). Colonies incubating eggs are quiet and consist almost entirely of females during the day. When eggs begin hatching, males reappear and assist in offspring provisioning. The periods of nest building (approximately two to four days), and incubation (twelve days) were previously established (Neff, 1937; Orians, 1961; Hamilton, pers. comm.; pers. obs.). Early observations of behavior at colonies therefore permitted me predict the day that hatching would begin.

Signs that hatching had begun included the peeping of young and provisioning flights by adults. During the first sampling visit, nests were marked with numbered flagging, and nestlings and eggs were counted. Due to the asynchronous hatching of tricolored blackbird clutches (a typical clutch of four eggs hatches over a period of three to four days (Hamilton, pers. comm.; pers. obs.)), contents of nests sampled on this visit consisted of both eggs and newly hatched young. A second visit was made three to five days after the first to monitor nest progress and again record the numbers of eggs and nestlings. The third and final visit was made on the eighth day after hatching began. Surviving offspring were counted and any eight day old offspring were weighed at that time. Weights were taken with a 100 gram Pescola spring scale and recorded to the nearest gram.

Assumptions about tricolors included in this study were 1) that partial clutch loss of hatched young was associated with starvation, and 2) that disappearance between visits of entire clutches was a consequence of predation on nestlings. These assumptions are supported by observations by Bowen *et al*. (1992) who could find no evidence supporting alternative explanations. For example, on numerous occasions, broad scale distributions of large numbers of dead nestlings on the ground around colony peripheries would appear between visits. These observations always coincided with decreases in the numbers of nestlings in sample nests along transects. Because the dead offspring were typically found half a meter or more from the edges of colonies, it was apparent that they had either died in the nest and were removed, or alternatively, were victims of brood reduction (Hamilton, pers. comm.). In either case, a pervasive intrinsic factor, most likely associated with starvation, was apparent.

Evidence that prefledging disappearance of whole clutches of tricolored blackbird nestlings was associated with predation includes direct and indirect observations of predator activity. On one occasion, black-crowned night herons (*Nycticorax nycticorax*) were observed taking large numbers of nestlings from a marsh colony (Hamilton, pers. comm.; pers. obs.). Prevalence of predation within marshes was also apparent by the unambiguous evidence of predator activities including the bent crowns of cattails over empty nests and mammal trails through marshes closely associated with empty pulled down nests. Further evidence that empty nests were usually the result of predation included only infrequent observations of isolated events: that is, empty nests within colonies occurred in patches (Hamilton, pers. comm.; pers. obs.). Finally, large avian, as well as mammalian predators would be expected to attempt to take all nestlings from a nest before furthering their search for prey. Because tricolored blackbirds do not defend nests in the presence of predators (pers. obs.), predators are virtually unhindered from taking entire clutches.

In this study therefore, where nests occupied on the previous visit were found empty, and evidence contradicting predator activity was absent, nestling mortality was attributed to predation.

Finally, where an entire clutch was lost but where the nestlings were found dead in the nest, the nest was recorded as abandoned, although death of the female parent, which would have produced similar results, may also have been the cause in some cases.

Data Analysis

Analysis was conducted using Systat statistical analysis software on an IBM PC compatible computer. One-Way ANOVA was used to test for between colony independence of variables. Where data was ordinal, such as for comparison of predation data across colonies, chi-square statistics were used. Spearman rank correlation coefficients were calculated to determine the degree of covariance between sample variables.

RESULTS

Clutch Size

Table 2 presents data for clutch sizes and hatching success. Clutch sizes ranged across colonies from a mean of 2.9 (SE = 0.75) eggs per nest to 3.7 (SE = 0.75) and were found to vary significantly ($P < 0.001$: $F = 5.681$). Few eggs failed to hatch (range = 0 to 2.8% of all eggs observed). Thus the number of hatchlings produced per nest was almost entirely a consequence of clutch size. There was, however, no significant correlation between mean clutch size and colony size ($r = -0.505$). See fig 1A.

Whole Clutch Loss

Predation and abandonment accounted for all whole clutch losses observed across colonies (22 and 78% of all whole clutch losses respectively). Predation at the marsh colony, (C6), was significantly higher than at any of the Himalaya berry colonies ($P < 0.01$: Chi-square = 18.57, df = 7), where 14 of 20 (73.7%) clutches of hatched offspring were preyed upon. See Table 3. Predation at the Himalaya berry colonies ranged from none observed at the smallest colony (C1) to four clutches of offspring at the largest (C8). Variation in predation rates were not found to be significant between the Himalaya berry colonies ($P > 0.25$: Chi-square = 1.93, df = 6). However, there was a strong correlation between the proportion of clutches preyed upon and colony size ($r = 0.982$) which was little changed when data from C6 was excluded from the analysis ($r = 0.929$). See fig 1B.

Nest abandonment occurred within four colonies. See Table 3. Five nests were abandoned across the four larger colonies compared to two among the smaller colonies. The difference however between the two groups was not significant ($P > 0.25$: Chi-square = 0.39, df = 1), and there was no significant correlation between the number of abandoned nests and colony size ($r = 0.386$).

Other causes of whole clutch failure included two nests at C7 to cattle grazing on the nest substrate and five at C6 to direct human disturbance by the property owner (Table 3). The latter were excluded from that colony's sample set for analytical purposes because the nests were lost immediately following the first visit. Thus the effective sample size for C6 was reduced from 25 to 20. At neither site did the events appear to affect the success of adjacent nests along the transects.

The difference in failure rates between the four larger and four smaller colonies when grouped was significant ($P < 0.001$, chi-square = 18.40, df = 1). In total, 29 of 95 nests (30.5%) between the four larger colonies failed to all causes compared to only five of 93 (5.4%) among the smaller colonies.

Partial Clutch Loss - Starvation

Starvation was pervasive across colonies. See Table 4. Because of the small number of surviving clutches at C6, data from that colony was excluded from the analysis where colonies were grouped for comparison of colony size effects. The proportion of clutches across colonies which experienced starvation ranged from 60.9% at C3 to 100% at C8. Mean offspring starvation ranged from 0.7 nestlings per nest (SE = 1.10) at C6 to 1.3 (SE = 0.91) at C4, but variation between colonies was not significant ($P > 0.1$, $F = 1.426$). There was also no correlation between starvation and colony size ($r = -0.041$) See fig 1C.

The actual proportions of offspring that starved per nest were also similar across colonies (range = 32.3% to 39.7%) and were not a function of colony size. See Table 4. When colonies were separated into groups by size the proportions of offspring starved were identical - 67 of 193 hatched offspring across colonies C5, C7, and C8 (34.7%) compared to 104 of 289 across C1, C2, C3, and C4 (35%) respectively.

Nestling Survivorship

Nestling survivorship is determined by clutch size minus nestling morbidity. Mean nestling survivorship (NS), which herein represents the average number of offspring per nest to survive to the eighth day after hatching began, ranged from 0.8 (SE = 1.18) to 2.3 (SE = 0.77) and differed significantly between colonies ($P < 0.001$, $F = 4.805$). Because starvation did not differ significantly across colonies, the pattern of results for NS (see Table 5) was more similar to that of predation effects (compare Tables 3 and 5). Figures 2A and 2B illustrate the functional relationships between NS and nestling predation and starvation respectively. NS was mostly a function of predation ($r = 0.694$), and data from C6 accounted for most of the variability. When data from that colony was excluded from the analysis, leaving only data from the Himalaya berry colonies for comparison, there was no significant difference in NS across colonies ($P > 0.05$, $F = 2.137$).

Nestling survivorship was also analyzed by excluding whole clutch failures, thereby including only nests for which at least one live young was present on the eighth day after hatching started (NSpartial). NSpartial thus reflected the combined effects of clutch size and nestling starvation. NSpartial ranged from 1.8 (SE = 0.72) to 2.6 (SE = 1.09) (see Table 5) and the difference across colonies was significant ($P = 0.4$, $F = 2.171$). NSpartial correlated more strongly with clutch size than nestling starvation ($r = 0.305$ and 0.142 respectively) though neither correlation was significant.

There were no significant colony size effects on NS or NSpartial observed ($r = -0.709$ and -0.512 respectively). See figs 1D and 1E.

Nestling Weight at Eight Days of Age

Weights of eight day old offspring ranged across colonies from a mean of 29.6 grams (SE = 2.31) to 40.5 grams (SE = 1.77) and differed significantly ($P < 0.001$, $F = 15.783$). See Table 6. There was, however, no significant correlation between nestling weight and colony size ($r = -0.473$) See fig 1F.

Variance in offspring weights between clutches, a measure which can be used as an indicator of parental competitive ability, was similar across colonies (see Table

6). Furthermore, variances were not correlated with the number of offspring surviving to the eighth day after hatching began (r = 0.329).

DISCUSSION

The results of this study demonstrate consistently high mean survivorship of nestling tricolored blackbirds in Himalaya berry habitat when compared to survivorship across marsh colonies (this study and those in Bowen *et al.* (1992), and Hamilton *et al.* (1995)). Nestling survivorship across Himalaya berry colonies included the highest observed in each of the years 1992 and 1993 for which comparable studies were conducted (Bowen *et al.*, 1992; this study; Hamilton, 1993). Beedy *et al.*'s (1991) conclusion that Himalaya berry habitat is suboptimal for breeding tricolored blackbirds is therefore rejected. Instead, the data strongly indicate that Himalaya berry thickets provide superior nesting substrate for tricolored blackbirds, and that the high suitability of that habitat is a consequence of significant reduction in predation pressure.

The low predation rates observed at Himalaya berry colonies in this study are consistent with those observed elsewhere, with only one exception (Bowen *et al.*, 1992; Hamilton, *et al.*, 1995). The intensity of predation observed at the single marsh colony in this study was similarly consistent with that from cattail marsh colonies in 1992 (Bowen *et al.*, 1992) and 1993 (Hamilton, 1993).

Among Himalaya berry colonies, nestling survivorship was mostly a function of starvation, the uniformity of which indicated that reproductive success was density dependent within colonies. These observations are similar to those of Bowen *et al.* (1992) and Hamilton *et al.* (1993) where starvation occurred in over 50% of observed nests within all colonies sampled. Within colony variation in nestling survivorship (when measured across only those clutches which survived to eight days after hatching began) and general nestling health was relatively high, indicating that parents were unequal in obtaining prey for offspring. However, the similarity of variances across colonies indicates that the proportions of parents of different competitive ability were more or less equal. An ideal free distribution model (Fretwell and Lucus, 1970; Fretwell, 1972), which includes unequal competitive ability (Parker and Sutherland, 1986), therefore appears to describe the distribution of breeding tricolored blackbirds, at least regionally where resource abundance, reflected in nestling starvation, is density dependent, and where starvation is unaffected by the number of competitors (colony size). Significant differences in nesting success between these colonies is largely a function of factors other than resource availability (e.g. predation).

The high incidence of predation at the marsh colony appeared to be habitat related. Great blue herons (*Ardea herodias*), another avian species associated with marshes, were the primary predator at that colony. Herons were observed foraging over the colony during the first two visits, and, by the third, the crowns of the cattail cover had been bent down over large portions of the marsh. All observed nests, including unmarked ones below trampled patches were empty. Evidence for predation at Himalaya berry colonies was circumstantial but indicative of the activities of small mammals such as cats, raccoons and skunks. Nests recorded as predated were tilted or completely destroyed. All were located in close proximity both to the ground (less than one meter high) and colony edges (within one third meters deep) and were thus within reach of mammalian predators. Evidence for the prevalence of predators around all Himalaya berry colonies, with the exception of C3, included numerous fresh tracks and scat, mostly from raccoons, one or both of which were observed upon all visits to the colonies. Despite the apparent abundance and proximity of potential predators, predation across the Himalaya berry colonies was relatively light. The morphology of Himalaya berry thickets appears to effectively discourage most animals including large avian species that would ordinarily prey on tricolored blackbird nestlings.

While mean nesting success was significantly lower at the marsh colony, individual success was among the highest observed. This appeared to be in part a function of the relatively large clutch sizes produced by that colony. The high nestling weights measured at that colony may have resulted from low competition for food resources as the nestling population was rapidly reduced by predation, or may have reflected proximity to abundant food supplies. In any case, poor overall nesting success at the marsh colony does not appear to be a function of population by inferior competitors.

While differences in predation rates across Himalaya berry colonies were not significant, the data appear to reflect at least a minor density dependent relationship between predation and colony size. This may indicate a greater abundance of mammalian predators around larger colonies, or alternatively, greater access to nests at larger colonies. Nest densities were qualitatively observed to be greater at the larger colonies. At the largest colony, densities appeared to be as great as five or more nests per cubic meter. Nest placement at colony edges itself does not appear to be density dependent however, as nests were located on edges at all colonies with the exception of the smallest colony.

The results of this study support the conclusions of Orians (1961) and Beedy *et al*. (1991) that habitat selection by breeding tricolored blackbirds is primarily driven by prey density with the additional requirement of nesting substrate in close proximity. This conclusion is further supported by a lack of evidence from this study that tricolored blackbirds distinguish predator risk between habitats. Himalaya berry habitat appears to meet the breeding requirements of tricolored blackbirds, yet in spite of the tendency of the species to use this habitat regionally, there is no indication of habitat preference: the marsh in this study was settled prior to completion of settlement at the Himalaya berry sites. Similar observations were made by Bowen *et al.* (1992) and Hamilton *et al.* (1995) where both habitats occurred. Behavioral traits, which select for distinct breeding habitats, do not appear to occur in the tricolored blackbird population unless unidentified subpopulations exist which discriminate in favor of Himalaya berry and possibly other upland habitats for breeding.

Conservation Considerations

The field efforts by Bowen *et al.* (1992) to evaluate the tricolored blackbird's status resulted in withdrawal of the state's petition to list the species as threatened or endangered. However, continued monitoring in the next few years may motivate resubmition of petitions. Meanwhile the tricolored blackbird is considered a species of special concern by the California Department of Fish and Game and efforts to develop a conservation plan are underway (Comrack, pers. comm.).

The value of this study to tricolored blackbird conservation is severalfold. First, it demonstrates the high suitability of Himalaya berry as nesting substrate relative to traditional marsh habitat. This creates an unusual situation for conservation biologists: Himalaya berry appears to present the first case where a weedy exotic plant species provides important habitat for a species of special conservation concern. The results of this study indicate that protection of Himalaya berry would be an important component of a viable conservation plan. Means to encourage tricolored blackbird use of Himalaya berry for breeding, for example, by increasing the abundance of such habitat, should also be seriously considered, at least in the short term. Himalaya berry has the added advantage that it is an aggressive perennial which could quickly and inexpensively be established anywhere throughout the tricolored blackbird's range. Increasing the abundance of Himalaya berry near otherwise suitable areas managed for tricolored blackbirds may significantly benefit the species' reproductive output, at least regionally, and thereby help to buffer the population as a whole against decline. Invasion by escaped Himalaya berry over portions of the tricolored blackbird's breeding range may have, at least in part, offset some of the species' population decline due to loss of former habitat since the early part of this century.

Another finding important for the conservation planning for tricolored blackbirds is the observation that mean nesting success across small Himalaya berry colonies may be as high or higher than larger ones. Thus, productivity across a comparably sized aggregate of small colonies may exceed that of a single large one. Efforts then to protect nesting tricolored blackbirds could potentially also include preserving portions of their range where suitable foraging habitat is available and where patches of nesting habitat are small but numerous and highly efficient. In other words, the value of small but highly productive colonies should not be underestimated.

Finally, the results herein, combined with those of Bowen *et al.* (1992), Hamilton (1993) and Hamilton *et al.* (1995), have proven southern Sacramento County to be a region of high tricolored blackbird productivity, and one that is therefore important to the species' survival. While on average only approximately a quarter of the population nested in Himalaya berry habitat between 1992 and 1994, over ninety percent of the colonies which did occurred in southern Sacramento County. It is conceivable, that in some years, successful breeding efforts may be largely confined to this region and a few others which contain somewhat similar upland habitats such as thistle stands. However, Himalaya berry thickets and associated foraging habitat is rapidly being consumed by development throughout Sacramento County (pers. obs.). Any possibility which might remain to preserve some of this landscape for tricolored blackbirds should be identified and addressed immediately.

COLONY	ADULT POPULATION SIZE	NEST SUBSTRATE	SETTLEMENT DATE	TRANSECT DATE	AGE OF OLDEST NESTLING (DAYS)
C8	15000	Himalaya berry	4/26/96	5/16/96	1
C7	3500	Himalaya berry	4/29/96	5/19/96	2
C6	3000	Cattails	4/24/96	5/14/96	1
C5	2400	Himalaya berry	5/03/96	5/23/96	1
C4	350	Himalaya berry	4/27/96	5/17/96	2
C3	320	Himalaya berry	5/02/96	5/22/96	1
C2	260	Himalaya berry	4/28/96	5/18/96	<1
C1	30	Himalaya berry	4/24/96	5/14/96	2

Table 1. Tricolored blackbird colonies sampled in 1993 in southern Sacramento County, California. Settlement date is the date that colonies became established. Transect dates are the dates that nests at colonies were first sampled. Oldest nestling age is the age of the oldest nestling across nests included in samples from each colony on the transect date.

COLONY	ADULT POPULATION SIZE	N	TOTAL NO. OF EGGS	MEAN CLUTCH SIZE	SE	NO. OF EGGS HATCHED	PERCENT HATCHED
C8	15000	25	80	3.2	0.74	78	97.5
C7	3500	25	73	2.9	0.75	73	100.0
C6	3000	20	92	3.7	0.75	90	97.8
C5	2400	25	74	3.0	0.78	74	100.0
C4	350	24	82	3.4	0.76	80	97.6
C3	320	24	76	3.2	0.84	75	98.7
C2	260	25	77	3.1	0.70	75	97.4
C1	30	20	72	3.6	0.77	70	97.2

Table 2. Clutch sizes and hatching success from eight tricolored blackbird colonies observed in 1993 in southern Sacramento County, California. The total number of eggs is the number of all eggs observed. N equals the number of nests sampled.

COLONY	N	NO. OF CLUTCHES PREYED UPON	PERCENT PREYED UPON	NO. OF NESTS ABANDONED	PERCENT ABANDONED	OTHER WHOLE CLUTCH FAILURES	PERCENT OF ALL NESTS THAT FAILED
C8	25	4	16.0	1	4.0	0	20.0
C7	25	2	8.0	2	8.0	2	24.0
C6	25	14	73.7	0	0.0	5	76.0
C5	25	2	8.0	2	8.0	0	16.0
C4	24	1	4.2	0	0.0	0	4.0
C3	24	1	4.2	0	0.0	0	4.0
C2	25	1	4.0	2	8.0	0	12.0
C1	20	0	0.0	0	0.0	0	0.0

Table 3. Whole clutch losses at eight tricolored blackbird colonies sampled in 1993 in southern Sacramento County, California. Colonies are listed from the largest to smallest number of breeding adults present. N is the number of nests sampled. The percent of nests preyed upon at C6 is calculated from the 20 nests remaining after 5 were lost to other causes.

COLONY	N	NO. OF EGGS HATCHED	NO. OF NESTS WHEREIN NESTLINGS STARVED	NO. OF NESTLINGS STARVED	PERCENT OF NESTLINGS THAT STARVED	MEAN NO. STARVED PER NEST	SE
C8	20	63	20	25	39.7	1.3	0.84
C7	19	55	14	20	36.4	0.8	0.79
C6	6	21	3	5	23.8	0.7	1.10
C5	21	65	18	21	32.3	1.1	0.95
C4	23	78	19	31	39.7	1.3	0.91
C3	23	73	14	22	30.1	0.9	0.91
C2	22	68	16	25	36.8	1.1	1.00
C1	20	70	18	24	34.3	1.1	0.59

Table 4. Starvation of nestlings across eight tricolored blackbird colonies observed in 1993 in southern Sacramento County, California. Included are only those nests sampled for which at least one nestling survived to the eighth day after hatching began. Colonies are ordered from the largest to the smallest number of breeding adults present. N is the number of nests sampled.

COLONY	ADULT POPULATION SIZE	N	MEAN NO. OF NESTLINGS SURVIVING PER NEST	SE	MEAN NO. OF NESTLINGS SURVIVING PER SUCCESSFUL NEST	SE
C8	15000	25	1.5	0.96	1.8	0.72
C7	3500	25	1.7	0.97	2.0	0.79
C6	3000	25	0.8	1.18	2.6	1.09
C5	2400	25	1.8	0.91	2.0	0.73
C4	350	24	1.9	0.82	2.0	0.75
C3	320	24	1.9	0.92	2.0	0.81
C2	260	25	1.7	0.97	1.9	0.87
C1	30	20	2.3	0.77	2.3	0.77

Table 5. Nestling survivorship at eight tricolored blackbird colonies observed in 1993 in southern Sacramento County, California. The mean number of nestlings surviving per nest was calculated including all nests. The second measure of nestling success, the mean number of nestlings surviving per successful nest was calculated excluding whole clutch losses such that only nests were included which contained at least one live offspring eight days after hatching began. N is the number of nests sampled.

COLONY	ADULT POPULATION SIZE	N	MEAN WEIGHT	SE
C8	15000	20	36.3	1.90
C7	3500	18	34.5	1.99
C6	3000	6	40.0	1.64
C5	2400	19	29.6	2.31
C4	350	18	30.5	1.89
C3	320	19	34.4	2.02
C2	260	18	36.7	1.67
C1	30	18	40.5	1.77

Table 6. Weights of eight day old tricolored blackbird nestlings taken at eight colonies in 1993 in southern Sacramento County, California. Weights were measured to the nearest gram. N is the number of nests sampled.

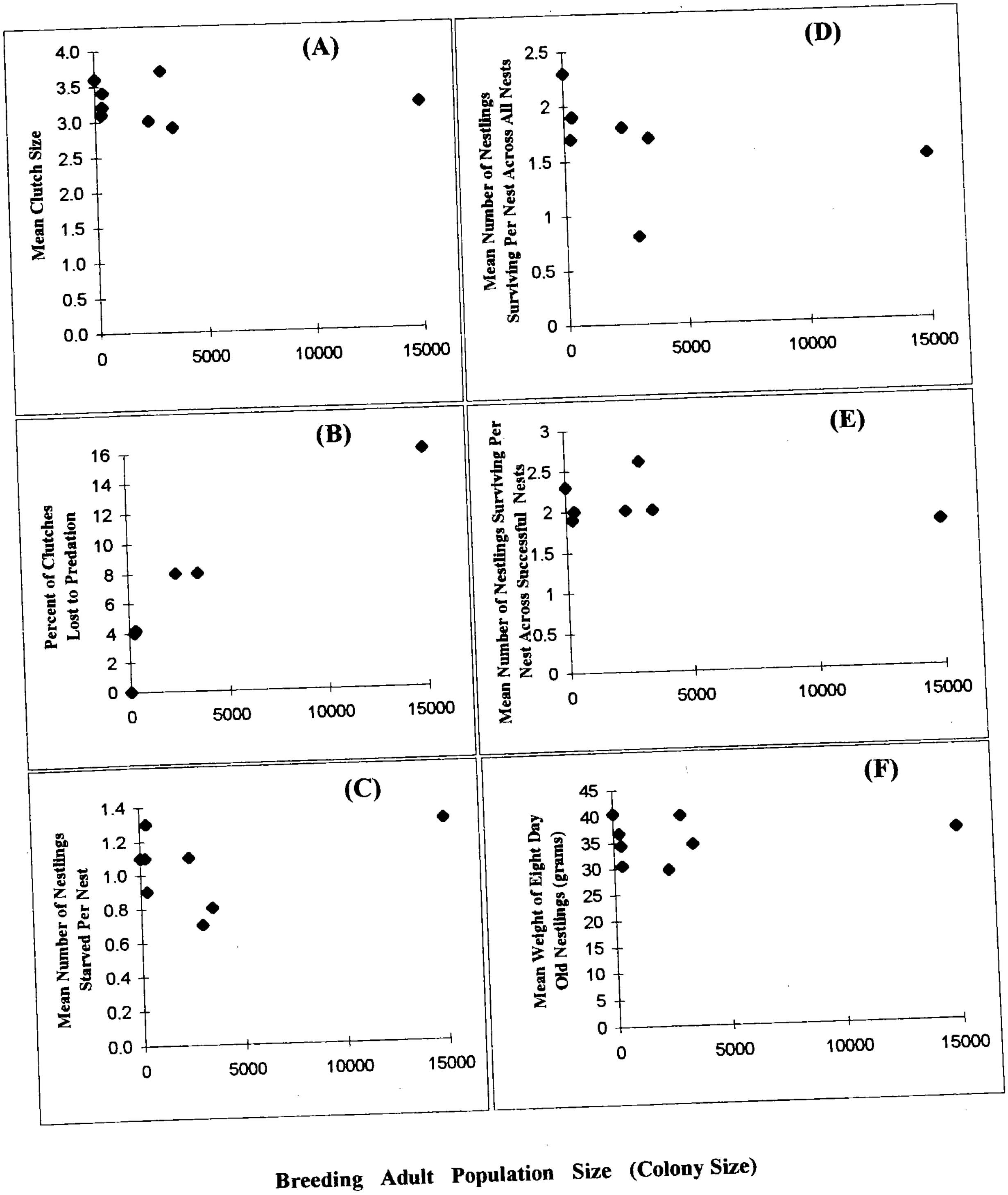

Fig. 1. Correlation plots of tricolored blackbird colony size with (A) mean clutch size, (B) percent of clutches lost to predation, (C) mean nestling survivorship across all nests at eight days after hatching began, (D) mean weight of eight day old nestlings, and (E) nestling survivorship across successful nests. Successful nests were only those from which at least one nestling survived to eight days after hatching began.

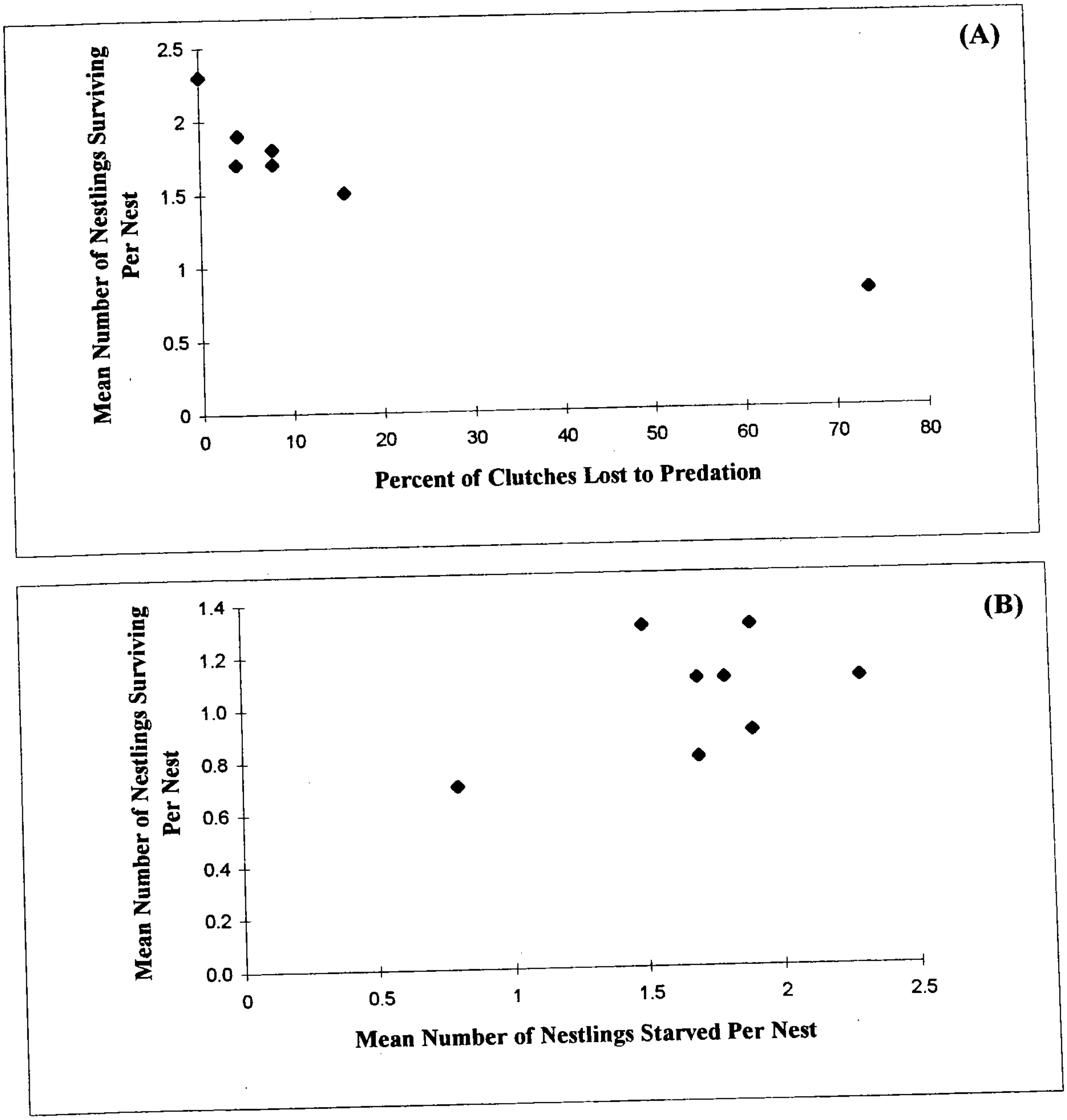

Fig 2. Correlation plots of tricolored blackbird nestling survivorship with (A) nestling predation and (B) nestling starvation. Mean number of nestlings surviving is the mean number surviving per nest on the eighth day after hatching began. Percent of clutches preyed upon involves all of those nests from which sudden entire clutch loss occurred because of predation of nestlings.

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