

technique to quantify their impact. This has been a major difficulty with studies of territoriality, which it is not a variable, but a constant within a given population. Consequently we may never be able to say that territoriality accounts for $x\%$ of the variance in population size, or that environmental factors account for another $y\%$. It is not enough to ask, "Does territoriality regulate population size?" Phrased in this fashion, the question is heuristically useless. Evolution has shaped the behavior of animals to permit flexible responses to ecological situations. As for our population, we conclude that social behavior in general, and territoriality in particular, had an impact on the number of Dippers on our study areas. The role of behavior on different sections of stream in different years was itself affected by feedback loops with other factors such as food, nest site quality and dispersion, age of birds, and total population size. Future studies must dissect these various relationships.

As King (1973) has noted, the proximate determinants of agonistic behavior are a complex series of interactions between intrinsic and extrinsic factors. Interrelationships between aggressive tendencies, population density, and environmental resources in the Dipper are not understood. We cannot say, for example, whether an individual Dipper was more or less aggressive in the presence of high food density, whether availability of roosts changed thresholds of agonistic behavior, or whether an abundance of cover allowed subordinate individuals to remain nearer dominant individuals. Dippers would be excellent subjects for experimental studies on the relationship of environmental variables to population density and aggression, but such studies remain to be done.

SURVIVAL AND PRODUCTIVITY

So far we have discussed population movements and the factors related to Dipper density and dispersion. During the breeding season these factors determined how many birds bred in an area and where they bred. However, they did not necessarily determine the actual size of the population. As Brown (1969b) has observed, the total size of a population may continue to rise by the addition of individuals to the floating component, even if the number of breeders remains fixed. Neglecting movements, the total size of the population is determined by the number of births minus the number of deaths in each year.

SURVIVAL AND MORTALITY

Survivorship and mortality rates are among the most difficult of all population parameters to study because of the confounding effects of dispersal. We had hoped that our populations would be relatively sedentary, but this was not the case. Our best estimate of adult survival comes from data on the number of breeding birds surviving from one breeding season to the next. Most nonbreeders present in the early spring months were in all probability first-year birds, and could not be relied upon to return the next year, even if they survived. Since none of the Dippers that bred on our study areas was ever observed to breed off the study area in subsequent years, we assumed that breeders had died if they were not observed the following year.

Our data on survival and estimates of survival rates are shown in Table 12. Survival of juveniles was estimated by assuming: 1) that just enough young survived to equal the number of new breeders on the study areas the following year,

TABLE 12
ESTIMATED SURVIVAL RATES OF ADULT AND JUVENILE DIPPERS

	1971	1972	1973
A. No. breeding birds	40	44	32
B. No. surviving from previous breeding season (% survival of adults) ^b	nd ^a (nd)	21 (52.5)	17 (38.6)
C. No. new breeders ^c	nd	23	15
D. No. fledglings banded	70	66	00
E. Estimated no. fledglings alive next spring ^d (estimated % survival of first-year birds) ^e	nd (nd)	23 (32.9)	15 (22.7)
F. Estimated total population ^f	110	110	nd
G. Estimated no. alive in next spring ^g (estimated % survival of population) ^h	nd (nd)	44 (40.0)	32 (29.1)

^a nd = data not available.

^b (Row B/row A) × 100.

^c Row A - row B.

^d Assumed = row C.

^e (Row E/row D) × 100.

^f Row A + row D.

^g Row B + row E.

^h (Row G/row F) × 100.

and 2) that the study areas were similar to other Front Range habitats in reproductive rate, mortality rates of adults and juveniles, and rates of immigration and emigration. These are the same assumptions used in the discussion of juvenile dispersal. While these are bold assumptions, they permit a rough estimate of survivorship. Annual adult survival rates from 1971–1972 and 1972–1973 were estimated at 52.5 and 38.6%. Juvenile survival rates were estimated at 32.9 and 22.7% in the same periods. Estimated annual survival rates for the population as a whole in the two years were 40.1 and 29.1%. We do not feel the quantity of data justifies estimates of survival by sex or study area.

These estimates of overall mortality are in general agreement with other studies. Farner (1955) estimated annual mortality in passerines at 40–70%; Lack (1954) estimated annual mortality rates of 40–60% for adult passerines and 82–92% from egg to breeding adult. Of an estimated 283 eggs laid on both of our study areas in 1971 and 1972, 38 were estimated to have reached breeding age, (Table 12E), an estimated 86.6% mortality. Robson (1956) estimated annual mortality of his Dipper population at 64.4%.

Little can be said about the timing or the causes of mortality. We suspect that predation was not an important cause of adult death. In 472 days in the field we witnessed only one attempt at predation on a Dipper, an unsuccessful attempt by a Sharp-shinned Hawk (*Accipiter striatus*). Recently fledged juveniles appeared to be less wary and probably were taken more often by predators. Johnson (1953) identified the remains of a fledgling Dipper in the stomach of a 25-cm brook trout (*Salvelinus fontinalis*). One juvenile banded in this study was found dead a month after fledging. Its remains were intact and dessicated, suggesting that death was caused by starvation, disease, or both.

Winter appears to have been the period of major loss for the population as a whole. Table 13 gives our data on population turnover from spring to subsequent fall (i.e., March to September) and from fall to spring (September to March). Losses over the two winters were significantly higher than those over the spring-

TABLE 13
RELATIVE LOSS OF DIPPERS FROM STUDY AREAS, SUMMER VS. WINTER

	1971	1972	Total
No. banded birds* in spring	65	63	128
No. spring birds seen in following fall	41	34	75
% birds lost over summer	36.9	46.0	41.4
No. banded birds in fall	99	80	179
No. fall birds seen in following spring	38	28	66
% birds lost over winter	61.6	65.0	63.1

* Only birds observed on study areas are included in this table.

summer periods ($P < 0.001$, both years' data; $0.025 > P > 0.001$, individual years, Chi-square test). Most of this loss was among juveniles and birds of unknown age, so there was a large emigration component to this "mortality" estimate. The fact that turnover was higher during the 1972 breeding season and summer (46.0% vs. 36.9% in 1971) when density was high (see Figs. 12, 13) suggests that losses were density-dependent. Without many more data it would be presumptuous to attempt a more detailed analysis of the rates and causes of losses from our population.

PRODUCTIVITY AND RECRUITMENT

The production of young to fledging was more easily observed than mortality. Table 14 presents data collected on several parameters of reproduction. There were surprisingly few differences between study areas and years for most of the parameters, and none of the logical comparisons was statistically significant. However, a few points are worth noting. Considering the population as a whole, 1972 was the year of highest population size and of poorest average reproduction. Only 50% of broods successfully fledged any young and the mean number of fledglings per brood was only 1.8. On South Boulder Creek the most likely cause of the poor performance was the silting and food decline in the upper three territories. On the Boulder Creek study area the number of breeding adults increased by 27% from 1971 to 1972, yet the number of fledglings per brood declined by 27%.

The total productivity (mean number of fledglings per brood times total number of broods) on both streams was estimated to have been 70 fledglings in both 1971 and 1972. However, the total breeding population increased 19% in the same period. In 1973 the total productivity declined to an estimated 42 fledglings, although the number of fledglings per brood rose 22% from the low of 1.8 in 1972. Because of the cold winter and delayed start of breeding, the number of second broods in 1973 was significantly lower than in 1972 and 1971 ($P = 0.008$, Fisher's exact test; Table 14 and Fig. 6), and the mean number of fledglings per adult female was also lower in 1973.

Table 15 lists data from this study along with data reported in the literature on reproduction in the family Cinclidae. The data from Dipper populations in the Boulder area appeared to be comparable to data from other studies in clutch size, percent of eggs fledging, and percent of broods fledging at least one young.

Factors affecting productivity

Lack (1954) and Cody (1966, 1971) have formulated a general theory of the selective forces operating on clutch size in birds, but the proximate determinants

TABLE 14
PRODUCTIVITY OF THE BOULDER AREA DIPPER POPULATION

Study area, data	1971	1972	1973	All years
A. Boulder Creek				
No. breeding adults ^a				
Males	9	13	8	30
Females	13	15	10	38
No. 1st broods	12	14	12	38
No. 2nd broods ^b	4	11	1	16
Total broods	16	25	13	54
Eggs/brood, mean \pm SD	4.6 \pm 0.5	4.3 \pm 0.8	4.2 \pm 0.9	4.4 \pm 0.8
(no. broods) ^c	(13)	(24)	(10)	(47)
Nestlings/brood, mean \pm SD	2.9 \pm 1.8	2.4 \pm 2.0	2.5 \pm 2.1	2.6 \pm 1.9
(no. broods) ^c	(15)	(24)	(10)	(49)
Fledglings/brood, mean \pm SD	2.6 \pm 1.7	1.9 \pm 2.1	2.0 \pm 1.9	2.1 \pm 1.9
(no. broods) ^c	(15)	(24)	(12)	(51)
Fledglings/adult female ^d	3.2	3.1	2.6	3.0
% Broods successful ^e	80.0	50.0	66.7	62.7
B. South Boulder Creek				
No. breeding adults ^a				
Males	7	7	6	20
Females	8	9	7	24
No. 1st broods	8	9	6	23
No. 2nd broods ^b	3	5	0	8
Total broods	11	14	6	31
Eggs/brood, mean \pm SD	3.7 \pm 0.8	4.4 \pm 0.7	4.6 \pm 0.6	4.2 \pm 0.8
(no. broods) ^c	(6)	(10)	(5)	(21)
Nestlings/brood, mean \pm SD	3.4 \pm 1.0	2.5 \pm 1.9	2.5 \pm 1.6	2.9 \pm 1.5
(no. broods) ^c	(10)	(10)	(6)	(26)
Fledglings/brood, mean \pm SD	2.6 \pm 1.4	1.7 \pm 2.0	2.5 \pm 1.6	2.2 \pm 1.7
(no. broods) ^c	(10)	(10)	(6)	(26)
Fledglings/adult female ^d	3.6	2.7	2.1	2.9
% Broods successful ^e	90.0	50.0	83.3	73.1
C. Both study areas				
No. breeding adults ^a				
Males	16	20	14	50
Females	21	24	17	62
No. 1st broods	20	23	18	61
No. 2nd broods ^b	7	16	1	24
Total broods	27	39	19	85
Eggs/brood, mean \pm SD	4.3 \pm 0.8	4.3 \pm 0.8	4.3 \pm 0.8	4.3 \pm 0.8
(no. broods) ^c	(14)	(34)	(15)	(68)
Nestlings/brood, mean \pm SD	3.1 \pm 1.5	2.4 \pm 1.9	2.5 \pm 1.9	2.7 \pm 1.8
(no. broods) ^c	(25)	(34)	(16)	(75)
Fledglings/brood, mean \pm SD	2.6 \pm 1.6	1.8 \pm 2.0	2.2 \pm 1.8	2.2 \pm 1.9
(no. broods) ^c	(25)	(34)	(18)	(77)
Fledglings/adult female ^d	3.3	3.0	2.4	3.0
% Broods successful ^e	84.0	50.0	72.2	61.8

^a Includes only pairs laying eggs.

^b Includes replacement broods.

^c no. broods = no. of broods used to calculate means and standard deviations.

^d [(mean no. fledglings/brood) \times (no. broods)]/no. adult females.

^e Success defined as fledging at least one young.

TABLE 15
REPORTED CLUTCH SIZES AND FLEDGING SUCCESSES FOR THE FAMILY CINCLIDAE

Cinclus species	Clutch size		Eggs fledged		Broods successful ^a		Location	Reference
	Mean	(n)	%	(n)	%	(n)		
<i>mexicanus</i>	4.3	(68)	56.5	(315)	61.8	(73)	Colorado, USA	This study
<i>mexicanus</i>	4.8	(4)	68.4	(19)	57.1	(7)	Montana, USA	Bakus (1959a)
<i>mexicanus</i>	4.1	(51)	68.8	(208)	66.7	(51)	Montana, USA	Sullivan (1973)
<i>cinclus</i>	4.7	(46)	50.6	(218)	61.4	(57)	Czechoslovakia	Balát (1964)
<i>cinclus</i>	4.1	(92)	75.0	(377)	nd ^b		Great Britain	Robson (1956)
<i>cinclus</i>								
Above 800'	3.7							
Below 800'	4.3	(>100)	61.6	(12)	nd		Great Britain	Shooter (1970)
<i>cinclus</i>	3.4 ^c	(9)	nd		nd		Great Britain	Hewson (1967)
<i>pallasii</i>	4 ^d	(nd)	nd		nd		Japan	Haneda and Koshihara (1967)

^a Success defined as fledging at least one young.

^b nd = data not available.

^c Biased by small sample and one female with unusually small clutches.

^d Modal clutch size, not mean.

of actual numbers laid are not understood (Cody 1971). In our study areas mean clutch size did not vary significantly (Table 14). The fact that productivity per adult declined when the total breeding population rose in 1972 suggests that resources might have been more limiting than in 1971. We expected a closer correlation between productivity and environmental parameters when population size was close to carrying capacity. Recall that there was a closer correlation between dispersion of birds and resources during periods of resource shortage (Tables 7, 8).

To analyze factors affecting productivity, the following variables were tabulated and punched onto Hollerith cards for each clutch (see Methods and Table 2 for methods of calculating indices and brief definitions of abbreviations): 1) clutch number (CLCHNUM), 2) elevation (ELEV), 3) age of male parent (MALEAGE), 4) age of female parent (FEMAGE), 5) sum of male and female ages (TOTALGEPR = MALEAGE + FEMAGE), 6) nest site quality (SITEQUAL), 7) height of nest site above water (SITEHITE), 8) date nest construction started (D8START), 9) date nest dome was completed (D8DOME), 10) date inner nest cup was completed (D8CUP), 11) date of first egg (D8EGGS), 12) clutch size (NOEGGS), 13) date incubation started (D8INCUB), 14) date eggs hatched (D8HATCH), 15) number of nestlings (NONESTL), 16) date of fledging (D8FLEDG), 17) number of fledglings (NOFLEDG), 18) size of female's territory (FEMTRSIZ), 19) mean food index of female's territory (MEANFOOD), 20) total food in territory (TOTFOOD = MEANFOOD × FEMTRSIZ), 21) presence or absence of at least one open end in territory (OPNENDS), 22) presence or absence of polygny (POLYGYNY), 23) mean stream flow in week before D8START (FLOB4CON), 24) mean stream flow during nestling period (FLONSTL), 25) mean minimum daily temperature during incubation (XMNTINC), 26) mean minimum daily temperature during nestling period (XMNTNSTL), 27) total precipitation during incubation (TPTNINC), 28) mean precipitation per storm during incubation (XPTNINC), 29) total precipitation during nestling period (TPTNSTL), and 30) mean pre-

TABLE 16
STEPWISE CORRELATION OF EIGHT VARIABLES WITH NUMBER OF FLEDGLINGS PER BROOD (1971-1973)^a

Step	Variable ^b	<i>r</i> of variable	<i>R</i> ² of step	<i>F</i> ratio of step	<i>F</i> ratio in final step
1	XPTNNSTL	-0.28*	0.08	3.30	11.55***
2	TOTAGEPR	0.22 ⁺	0.22	5.64*	3.34*
3	NOEGGS	0.25 ⁺	0.28	4.92*	5.59***
4	FEMTRSIZ	0.06	0.34	4.76**	3.61**
5	XMNTINC	-0.20 ⁺	0.38	4.34**	1.16
6	POLYGYNV	-0.14	0.39	3.70*	1.82
7	MEANFOOD	0.11	0.41	3.32*	4.51**
8	SITEQUAL	0.09	0.47	3.64**	3.78**

^a *n* = 42 (listwise deletion used).

^b FEMTRSIZ, size of female's territory; MEANFOOD, mean of interpolated food at 100-m intervals in territory; NOEGGS, clutch size; POLYGYNV, presence or absence of polygyny; SITEQUAL, nest site quality index; TOTAGEPR, sum of ages of male and female; XMNTINC, mean minimum daily temperature during incubation; XPTNNSTL, mean precipitation per storm during nestling period.

⁺ *P* < 0.10, * *P* < 0.05, ** *P* < 0.01, and *** *P* < 0.001.

precipitation per storm during nestling period (XPTNNSTL). The data were submitted to a Pearson product-moment correlation program to obtain a correlation matrix. Point biserial coefficients were calculated as the best estimates of correlations between dichotomous variables (OPNENDS, POLYGYNV) and continuous variables; a phi coefficient was calculated and inserted as the best estimate of the correlation between the dichotomous variables (Ferguson 1971). These were inserted into appropriate rows and columns of the matrix. Preliminary analysis indicated that the best variables for predicting NOFLEDG were: SITEQUAL, TOTAGEPR, NOEGGS, FEMTRSIZ, MEANFOOD, POLYGYNV, XPTNNSTL and XMNTINC. These eight variables were used in stepwise correlations to determine their relationship with number of fledglings.

Table 16 summarizes the results of the first stepwise regression using data from both study areas and all three years (1971 Boulder Creek data were deleted because of inadequate data on territory size). Taken together, the eight variables accounted for 47% of the variance in number of fledglings per brood, and the overall correlation coefficient was significant at the 0.01 level.

XPTNNSTL was the most powerful single predictor variable and accounted for 8% of the variation in NOFLEDG. Storms with large amounts of precipitation flooded some nests and hindered adult foraging by raising water levels and increasing turbidity.

With the effect of the first predictor removed, TOTAGEPR was the strongest variable and added 14% to the multiple *R*² (Table 16). Older, more experienced pairs tended to have better fledging success than younger pairs. Age of female may be more important (*r* = 0.15, *P* > 0.30) than male age (*r* = 0.06, *P* > 0.60). However, this cannot be confirmed from our data, for the two coefficients do not differ significantly (*P* > 0.50). Interestingly, MALEAGE was negatively correlated with females' territory sizes (*r* = -0.14, *P* > 0.30) and food density (*r* = -0.27, 0.10 > *P* > 0.05), but positively correlated with nest site quality (*r* = 0.35, 0.05 > *P* > 0.01). It is not surprising that older males occupied better sites than younger males, but one might expect older males to have larger territories and more food. High-quality sites occurred most often in steep portions of canyons with many cliffs and bridges, and low food densities. The negative correlation of mean food

and site quality was especially strong ($r = -0.67$, $P < 0.001$). It is likely that there was strong competition for sites in these areas despite low food densities. Older males appear to have been better able to compete for these sites and thus their territories tended to be small because of the presence of adjacent males' territories. These data suggest that, on our study areas, good nest sites were more important than food to birds choosing territories.

NOEGGS and FEMTRSIZ, the third and fourth predictors entered, were both positively correlated with number of fledglings and increased the amount of variance explained to 28 and 34%, respectively. Whereas FEMTRSIZ alone was not significantly correlated with number of fledglings, removing the effects of XPTNSTL, TOTAGEPR and NOEGGS resulted in a significant partial correlation of FEMTRSIZ with number of fledglings ($r_p = 0.29$, $0.10 > P > 0.05$).

Unexpectedly, XMNTINC was negatively correlated with number of fledglings ($r = -0.20$, $P < 0.10$). Low temperatures during incubation would increase the females' energy expenditures and require them to spend more time foraging during a period when eggs would cool rapidly. This would be more important for Dippers than for species where males assist in incubation. Low fledging success associated with low temperatures should produce a positive correlation coefficient. We believe this relatively high negative correlation was due to a combination of other variables and is probably an artifact. The computer program which produced the results shown in Table 16 used a "listwise deletion" option which omitted any case with incomplete data (i.e., clutches lacking data for any of the nine variables). This resulted in elimination of 33 cases from the calculations. When all data were used ("pairwise deletion"), the correlation between these two variables dropped to -0.09 ($n = 66$, $P > 0.20$). This difference of 0.11 between the listwise and pairwise correlation coefficients was unusual. The correlation coefficients of the other seven variables with number of fledglings were more stable; they changed an average of only 0.06 when list- and pairwise correlation coefficients were compared.

Another complication arose from the fact that minimum temperature was highly correlated with time of breeding ($r = 0.90$, $n = 68$, $P < 0.001$), while number of eggs was significantly and negatively correlated with date of the first egg ($r = -0.21$, $n = 75$, $0.05 > P > 0.02$). The first-order partial correlation of XMNTINC with number of fledglings (controlling for NOEGGS) was -0.07 ($n = 63$, $P > 0.25$), indicating that part of the negative correlation of minimum temperature with number of fledglings may have been due to the decline in clutch size as the breeding season progressed. The temperatures during our study may have had an effect, but it cannot be discerned from this analysis because of difficulties with the particular sample and with confounding variables. Dippers have a low minimum critical temperature (Murrish 1970b) and we expect temperatures to have relatively less effect than on many other species.

POLYGYNY was also negatively correlated with number of fledglings. In an earlier analysis of two years' data on polygyny in the Dipper, we suggested that reproductive success of polygynous birds was higher than the success of monogamous ones (Price and Bock 1973). In the three years of this study, polygynous males fledged significantly more young than monogamous males (polygynous mean = 6.11, monogamous mean = 3.31; $0.01 > P > 0.005$; t test). Polygynous females fledged insignificantly fewer young than monogamous females (polygy-

TABLE 17
 MULTIPLE AND STEPWISE CORRELATIONS OF GROUPED VARIABLES WITH NUMBER OF
 FLEDGLINGS PER BROOD (1971-1973)^a

	Total R^2 of group alone	R^2 of groups in steps (increment)
A. Territory quality variables ^b		
SITEQUAL		
FEMTRSIZ		
MEANFOOD		
POLYGYNY	0.13	0.13 (0.13)
B. Weather variables		
XPTNNSTL		
XMNTINC	0.13	0.26 (0.13)
C. Other variables		
TOTAGEPR		
NOEGGS	0.09	0.47** (0.21)

^a $n = 42$.

^b FEMTRSIZ, size of female territory; MEANFOOD, mean interpolated food at 100-m intervals in territory; NOEGGS, clutch size; POLYGYNY, presence or absence of polygyny; SITEQUAL, nest site quality index; TOTAGEPR, sum of male and female ages; XMNTINC, mean minimum daily temperature during incubation; XPTNNSTL, mean precipitation per storm in nesting period.

** $P < 0.01$.

nous mean = 3.06, monogamous mean = 3.22; $P > 0.50$). For our three years' data, the point biserial correlation coefficient of polygyny with number of fledglings was -0.14 ($n = 75$; $P > 0.50$).

MEANFOOD and SITEQUAL were positively associated with number of fledglings. Nests in high-quality sites were less likely to fall off a ledge or to be destroyed by predators or high water. High food density enabled parents to keep up a high feeding rate because food could easily be found. We should note again that the food data used in this analysis were taken in the spring of 1973, so this probably is an underestimate of the importance of food.

It is perhaps surprising that the two factors we believe were most important in the choice of breeding site (food and site quality) entered the correlations late. Evidently Dippers rarely chose to breed at poor sites in areas seriously deficient in food. This is an example of the difficulty of analyzing complex feedback loops which affect reproduction and population size. Below a threshold of food density and/or nest site quality, it is unlikely that Dippers will attempt to breed. Resource levels just above the threshold, such as barely adequate food availability, may be compensated for by other factors, such as a larger territory. Abundant resources may allow for much reduced territory sizes. Once a territory is established, stochastic factors, such as weather, may be of major importance.

The computer programs used in this analysis allowed us to group variables together. Table 17 shows the eight variables placed into three groups for analysis. The first cluster (Table 17A) includes four variables which could be said to characterize territory quality. The second group (Table 17B) includes measures of the effects of two weather variables on breeding success. Finally, clutch size and parental age are placed separately (Table 17C) because they are, to some extent, intrinsic to the birds themselves. These three groups are, of course, not completely independent. The quality of a bird's territory is determined in part by intrinsic factors such as the bird's aggressiveness and its skill in assessing the environment. The components of territory quality and weather accounted for equal and inde-

TABLE 18
 MULTIPLE AND STEPWISE CORRELATIONS OF GROUPED VARIABLES WITH NUMBER OF FLEDGLINGS PER
 BROOD FOR SUBSETS OF DATA

Data subset (<i>n</i>)	Variable group	Variable ^a	<i>r</i> of variable	Total <i>R</i> ² group alone ^b	<i>R</i> ² of step in stepwise correlation ^b	
A. Both study areas, 1972, 1973 (33)	Territory quality	SITEQUAL	0.07	0.17	0.17	
		FEMTRSIZ	0.07			
		MEANFOOD	0.17			
		POLYGYNY	-0.17			
	Weather	XPTNNSTL	-0.34 ⁺	0.19 ⁺	0.34	
		XMNTINC	-0.25			
	Other	TOTAGEPR	0.23	0.13	0.65 ^{***}	
		NOEGGS	0.31			
	B. Both study areas, 1972 (20)	Territory quality	SITEQUAL	0.23	0.63 ^{**}	0.63 ^{**}
			FEMTRSIZ	0.19		
MEANFOOD			0.16			
POLYGYNY			-0.31			
Weather		XPTNNSTL	-0.39 ⁺	0.21	0.74 ^{**}	
		XMNTINC	-0.26			
Other		TOTAGEPR	0.20	0.31 ⁺	0.88 ^{***}	
		NOEGGS	0.47 [*]			
C. Both study areas, 1973 (13)		Territory quality	SITEQUAL	-0.19	0.12	0.12
			FEMTRSIZ	-0.17		
	MEANFOOD		0.18			
	POLYGYNY		0.12			
	Weather	XPTNNSTL	-0.38	0.17	0.34	
		XMNTINC	0.07			
	Other	TOTAGEPR	0.29	0.13	0.81	
		NOEGGS	0.29			
	D. Boulder Creek 1972, 1973 (21)	Territory quality	SITEQUAL	0.46 [*]	0.34	0.34
			FEMTRSIZ	0.11		
MEANFOOD			0.13			
POLYGYNY			-0.15			
Weather		XPTNNSTL	-0.31	0.15	0.55 ⁺	
		XMNTINC	-0.21			
Other		TOTAGEPR	0.42 ⁺	0.20	0.91 ^{***}	
		NOEGGS	0.33			
E. Boulder Creek 1972 (13)		Territory quality	SITEQUAL	0.58	0.61	0.61
			FEMTRSIZ	0.32		

TABLE 18
CONTINUED

Data subset (<i>n</i>)	Variable group	Variable ^a	<i>r</i> of variable	Total <i>R</i> ² group alone ^b	<i>R</i> ² of step in stepwise correlation ^b
		MEANFOOD	0.09		
		POLYGyny	-0.29		
	Weather			0.17	0.80
		XPTNNSTL	-0.24		
		XMNTINC	-0.20		
	Other			0.34	0.93 ⁺
		TOTAGEPR	0.39		
		NOEGGS	0.38		

^a FEMTRSIZ, size of female's territory; MEANFOOD, mean of interpolated food at 100-m intervals in territory; NOEGGS, clutch size; POLYGyny, presence or absence of polygyny; SITEQUAL, nest-site quality index; TOTAGEPR, sum of ages of male and female; XMNTINC, mean minimum daily temperature during incubation; XPTNNSTL, mean precipitation per storm during nestling period.

^b Significance levels based on *F* ratios.

⁺ $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

pendent amounts of the variation in fledging success. By themselves, number of eggs and age of parents accounted for only 9% of the variance in number of fledglings per brood (Table 17C). However, NOEGGS and TOTAGEPR almost doubled the amount of variance explained by the other two groups when all three groups were used together.

This analysis demonstrates that territory quality and weather, along with birds' physiological condition and genotype (i.e., age, clutch size) were important factors in determining the number of young fledged per brood. However, the amount of variation in fledging success explained by these variables was only 47% (Tables 16, 17). In our discussion of factors affecting population density and dispersion we predicted a high correlation between density and environmental resources during the reproductive season. Multiple R^2 's of various environmental factors with dispersion of breeding adults were greater than 0.47 in four of the five analyses performed. A number of factors contributed to the low overall correlation with NOFLEDG. If each of the years and study areas was different from the others in some systematic way (e.g., stream flow, population density, temperatures), we might expect the differences to even out when years were analyzed together. Also, in the absence of better data, the food measured in 1973 was used for 1971 and 1972.

To avoid some of these problems we performed analyses on several subsets of the data (Table 18). Stepwise correlations are shown for data from both study areas in 1972 and 1973 together, 1972 and 1973 separately, Boulder Creek in 1972 and 1973 together, and Boulder Creek in 1972 alone. Other subsets of data were too small for meaningful analysis.

The results support our hypothesis that the previous correlations were done on data that were not comparable. With all 1971 data removed, the multiple coefficient of determination was 0.65, whereas R^2 for the 1972 data was 0.88 and 0.81 for the 1973 data (Table 18A, B, C). When analysis was restricted to a single study area (Boulder Creek), the resulting correlations were even higher for 1972 and 1973 together, and for 1972 alone (Table 18D, E). These results support our contention that the factors "regulating" the productivity of our populations differed from year to year and from one study area to the other. Combining data

from the Boulder and South Boulder study areas obscured processes which operated independently on each area.

Our samples are too small for rigorous tests, but some general comments are worthwhile. For example, 1973 was wetter in April and May than 1972 (Fig. 4). The correlation of XPTNNSTL with NOFLEDG was higher than that of any other variable in 1973, but was less outstanding in 1972 (Table 18B, C). On the other hand, the population densities on our study areas were higher in 1972 than in 1973 (Figs. 12, 13) and we believe that competition for territories, food, nest sites, and mates was higher in 1972 (Fig. 16, Table 11). Correlations of territory-quality variables with number of fledglings were generally higher in 1972 than in 1973 (Table 18B, C). MEANFOOD was the only exception. This is not surprising, considering that food data from 1973 were used for all correlations. The multiple correlation for the four territory-quality variables was much higher in 1972 ($0.10 > P > 0.05$, Fisher's z transform and t test). Comparisons of the Boulder Creek study area with the South Boulder Creek study area would be most interesting; however, as mentioned in the section on dispersion, our South Boulder Creek sample was small and there were several unusual problems on the study area (silting, polygyny).

Proximate causes of nesting failure

The immediate causes of nesting failure usually were difficult to pinpoint, but we do have data from 31 closely-watched broods. Eight (26%) were abandoned (one female is known to have died and two broods were abandoned by adults that later bred elsewhere). Eleven (36%) were destroyed, seven (23%) by flooding and three (10%) probably by humans. One brood (3%) probably starved, for the nest was in the area of South Boulder Creek where silting occurred in 1972. Disease cannot be ruled out, however. Several dead broods off the main study areas were autopsied by personnel of the Denver Zoological Garden and diagnosed as having died of aspergillosis. Four broods on the study areas were heavily infested with feather lice (Mallophaga) but all fledged apparently normal young. Three broods failed because the female may have been sterile. She laid three clutches over two years; all either failed to hatch or died soon after hatching. (Those that hatched did so only after abnormally long incubation periods.) The two males involved were polygynous and sired other broods successfully. Finally, a pair of Dippers flew into an adjacent territory after the male abandoned it and were observed pecking into the abandoned female's nest and pulling it apart. No fledglings were seen from this nest and it is likely that the nestlings were killed. The remaining seven broods (23%) failed for unknown reasons.

EFFECT OF STOCHASTIC EVENTS IN SURVIVAL AND PRODUCTIVITY

There has been considerable debate in the literature over the role played by "density-independent," random factors in the dynamics of natural populations (Andrewartha and Birch 1954, Lack 1966). Theoretical models of population processes have shown that stochastic processes may have considerable impact (e.g., Crow and Kimura 1970, Gadgil 1971). Of particular importance are catastrophic events that decimate populations or their habitat. Although no major disasters occurred during our study, there are data to indicate that Front Range Dipper populations are subject to occasional catastrophes.

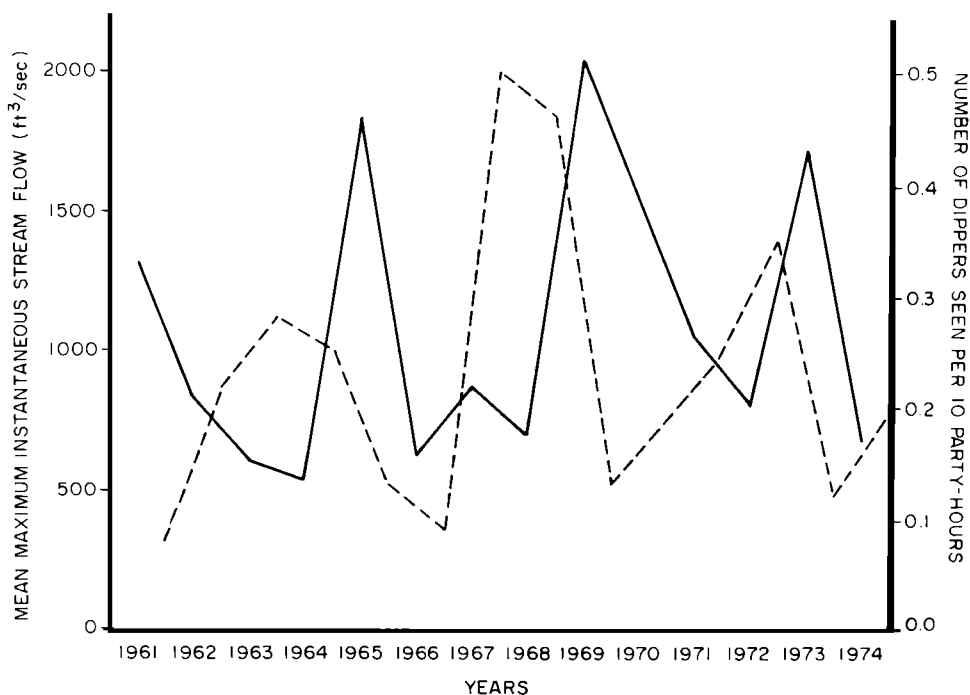


FIGURE 17. Relationship of winter densities to stream flow in spring. (The dashed line indicates mean number of Dippers seen in Boulder area Audubon Christmas Counts, 1961–1974, Audubon Field Notes, vols. 17–24, and American Birds, vols. 25–28; the solid line indicates the mean maximum instantaneous flow of six Boulder area streams in the previous spring, Colo. Dept. Water Resources, pers. comm.)

Because flooding was a major cause of nesting failure, we studied the relationship of flooding to population size. We tabulated the number of Dippers seen in 14 consecutive winters and correlated them with previous springs' runoff of local streams. Population sizes were based on six Audubon Society Christmas Bird Counts from 1961 to 1974 (Fort Collins, Rocky Mountain Park near Estes Park, Longmont, Boulder, Idaho Springs, and Denver); the runoffs were of six local streams (St. Vrain, Boulder, South Boulder, and Clear Creeks, and Big Thompson and South Platte Rivers). The results of this analysis are shown in Fig. 17.

There was a clear tendency for the number of Dippers seen in winter to decline following springs with high runoff ($r = -0.58$, $n = 14$, $0.05 > P > 0.02$). Maximum stream flow almost invariably occurred during the nesting season and is probably the best predictor of impact of stream flow on Dipper populations, for none of our streams dried up.

It is worth noting that the various rivers did not fluctuate synchronously. Not surprisingly, closely adjacent streams tended to be most closely correlated ($r > 0.70$), with lower correlations ($0.50 > r > 0.10$) between more widely separated streams. The South Platte did not correlate closely with other streams. Although the South Platte receives the others, the gauging station from which these data were taken was located at Kassler (Fig. 1), far upstream of the junction of the South Platte with the other drainages.

In 1965 the South Platte River flooded and caused millions of dollars damage, but Boulder Creek and the Big Thompson did not flood. The reverse occurred in 1969 when the streams north of Clear Creek flooded, but not the South Platte upstream of Denver (Colo. Dept. of Water Resources, pers. comm.). The Whitneys (1972, pers. comm.) noted that the 1969 flood drastically reduced Dipper fledging success in the St. Vrain drainage. In late July 1976 the Big Thompson River had a record flood, but none of the other streams flooded significantly.

Floods affect Dippers in several ways. They wash away poorly placed nests. High, turbid water kills many stream organisms (Mecom 1969) and makes the remainder harder to find. Poor nutrition of adults and nestlings would reduce the growth rate of young and increase the susceptibility of adults and young to mortality from many causes.

Although the occurrence and severity of floods are not related to population density, their effect on the population would, in part, depend on population density. At high densities a greater proportion of the breeding birds occupied poor territories and nest sites (Fig. 16) and thus larger numbers would be affected by flooding. Severe floods could reduce the local carrying capacity for several years until the bed stabilized and stream fauna recovered.

The silting on South Boulder Creek in 1972 and the short 1973 breeding season also illustrate effects of stochastic events on breeding. Heavy silting significantly reduced Dipper productivity on the South Boulder study area. In the upper 4 km of the study area only four young were fledged in 1972, compared with 21 in 1971 ($P < 0.01$, t test of mean fledging success). It is worth noting that Dippers normally persist with a breeding attempt even under adverse circumstances (see Alder, 1963, for an example). Of 12 females that lost first broods elsewhere in our study areas, nine renested; none of the four females in the silted area did so ($P = 0.01$, Fisher's exact test).

Unusual temperatures may also affect Dipper populations, although data comparable to those on streamflow and winter densities are difficult to find. Temperatures in the breeding season affect melting of snow and thus stream flow, as well as the thermal physiology of the birds. We cannot measure these effects, however. Winter temperatures would influence the extent of ice formation and Dippers' metabolic rates, and thus winter mortality and population density. An example may have been the winter of 1972–1973, which was unusually early and cold (Fig. 4). The 1973 breeding population was smaller than in 1971 or 1972 (32 vs. 40 and 44) and had a lower percentage of birds surviving from previous years than in 1972 (29.1% vs. 40.0%). We believe that much of the high mortality was due to the low temperatures that winter. After the hard winter of 1972–1973, the 1973 breeding season was much shorter (from first egg laid to last brood fledged, 88 days vs. 131 days in 1971 and 134 in 1972) and there were significantly fewer second broods than in other years (Fig. 6; Table 14; $P < 0.005$, Chi-square test).

From these data it is clear not only that spring floods and winter weather can seriously affect survival and productivity, but that in the Colorado Front Range such catastrophes may be quite local. Dipper habitats in the Front Range may be characterized as patchy, with asynchronously fluctuating carrying capacities. The birds themselves use the environment in a more coarse-grained manner (Pianka

1974) than other Dipper populations reported in the literature. The fact that our population was more mobile than others confirms Gadgil's (1971) hypothesis that these conditions should lead to high dispersal rates.

DISCUSSION OF SURVIVAL AND PRODUCTIVITY

We conclude that survival and reproduction of Dipper populations are heavily dependent on a number of factors that are both intrinsic and extrinsic to the birds themselves, and that may or may not be responsive to density.

Adult mortality was highest in winter and probably was due to the severity of winter weather, to the extent of ice formation, and to winter population density. Adults had higher survival rates than first-year birds. While adults did not appear to be vulnerable to predation, this may not have been true of juveniles, which appeared to be less wary. Although the freezing of streams was not affected by Dipper density, the resulting population density in winter was in part determined by survival and productivity in the previous spring. It appears that at high densities more individuals were forced by aggression to move to other streams, and hence to be more vulnerable to death from many causes. Thus, the proportion of the population which died because of severe weather may well have been a function of population density.

Reproduction in Dipper populations was heavily dependent on environmental factors and on the quality of the adults' territories. Probably the major factors affecting productivity were those relating to stream flow (precipitation, temperature), food availability (stream flow, food density, territory size, bottom structure), nest security (probability of flooding, accessibility to predators), and timing of breeding (weather). Winter and early spring weather were important and unpredictable determinants of timing of breeding, and hence the number of second broods. Weather during spring affected water levels, and hence accessibility of food and probability of nests being flooded. Local flooding increased the difficulty of foraging as well as the amount of food available. Cold, wet weather increased food and shelter requirements of both adults and young, and made those resources more difficult to obtain. The quality of the birds' nest sites and territories had much to do with how severely high water and weather affected their reproductive output. Population density and territorial behavior affected reproduction at high densities by forcing more individuals to move off the study areas or to accept poor-quality nest sites and territories.

GENERAL DISCUSSION AND CONCLUSIONS

After individual analyses of the major parameters of the Front Range Dipper population, we are in a position to discuss what "regulates" that population and to assess the general significance of our study. Ecologists have proposed a number of hypotheses to explain the dynamics of animal populations. It is not our intention to comprehensively review the enormous literature on this subject; for this the reader should consult such works as Watson (1973), Dempster (1975), Southwood (1975), or a recent ecology text such as Ricklefs (1979). Tamarin (1978) provides an excellent anthology on this topic. We will briefly review our findings regarding the major influences on our population, then discuss their relevance to the study of population dynamics.