

DISTRIBUTION, ABUNDANCE, AND SURVIVAL OF NESTING AMERICAN DIPPERS NEAR JUNEAU, ALASKA

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ABSTRACT: We studied the distribution of the American Dipper (*Cinclus mexicanus*) near Juneau, Alaska, from 2004 through 2008. An upper limit on the local abundance and distribution of dippers in our area resulted from several factors, including stream size and food abundance, nest sites, and territorial aggression. Dippers nested only along streams with an estimated flow in summer of at least 0.5 cubic feet per second and nested commonly only where flow exceeded 0.9 cubic feet per second. Large streams provided a greater average density and estimated total abundance of benthic macroinvertebrates. Although most territories were centered on typical fast, rocky reaches of fairly high gradient, a few were centered on low-gradient reaches with a sandy substrate where anthropogenic nest sites were available. Some nests were located along glacial streams, but no nests were located along streams originating in bogs. Nest sites were typically in locations protected from predators, floods, and other hazards. After each of three cold winters apparent survival was low, markedly reducing the number of occupied territories; survival analysis with the program MARK showed that apparent survival decreased with decreasing winter temperature. We suggest that if dippers are used as indicators of stream quality in our area, the research should either include multi-year and region-wide surveys of distribution and abundance to account for annual variation in survival or focus on the effects of stream pollution on dipper physiology and reproduction.

The American Dipper (*Cinclus mexicanus*) is North America's only aquatic songbird. It nests along streams in the mountainous regions of western North America from northern Alaska to Central America and feeds on aquatic invertebrates and small fish (e.g., Kingery 1996, Willson and Hocker 2008b). The distribution and abundance of the dipper are often considered to be limited mainly by the availability of suitable nest sites or sometimes also by food supply (e.g., Kingery 1996). Here we consider the roles of these and other factors in limiting the distribution and abundance of dippers near Juneau, southeastern Alaska. We compare the presence of nesting dippers with estimates of stream size and prey abundance and characterize the core portions of nesting territories and specific nest sites. We then report variation in annual survival and its effect on territory and stream occupancy.

The five species of dippers can be used as indicators of stream quality because their abundance or reproductive success often decreases in response to acidification, sedimentation, or industrial pollutants (e.g., Tyler and Ormerod 1994, Price and Bock 1983). Near Juneau, streams are subject to several kinds of natural and anthropogenic disturbances (e.g., Redman 1988, Swanson et al. 1998), such as mining, logging, and road building, that can affect their quality. Therefore, a baseline understanding of dipper distribution and abundance is useful for understanding and assessing future patterns. We here provide a baseline for future comparisons of the distribu-

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tion and abundance of the dipper near Juneau and discuss the species' use as an indicator of stream quality.

STUDY AREA

Our study area is located near Juneau (58° 18' N 134° 25' W) in southeastern Alaska. During the nesting season, we searched for dippers along 40 streams from Pt. Bishop north to Bessie Creek on the mainland (a distance of approximately 93 km along the coast) and around nearby Douglas Island (approximately 77 km of coast; Figure 1). Ten of the streams that we studied are second-order, four are third-order, and the remainder are first-order, as judged from a topographic map (1:63,360). Most of these streams originate

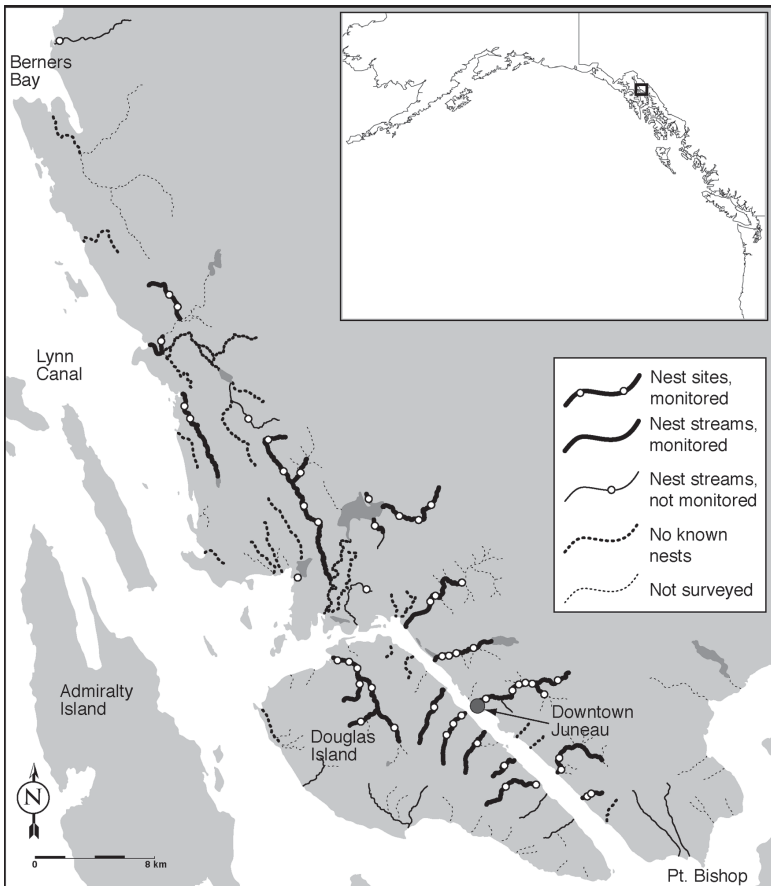


Figure 1. The study area around Juneau, Alaska, showing streams surveyed and approximate locations of nest sites occupied in at least one year of the study.

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in alpine zones and are fed largely by snow melt in spring and summer. Three streams originate at glaciers, nine originate in mid-elevation bogs, and two originate in natural nonglacial lakes. Seven of these streams were accessible only by boat, and we visited them only once; we include these streams only in the characterization of occupied and unoccupied watersheds. The remaining 33 streams were accessible within a 3- or 4-hour round-trip hike from local roads. This set of streams we surveyed regularly includes all streams in the Juneau area except the three largest glacial rivers, mostly at a low gradient, and tiny intermittent streams. Initial surveys quickly showed that such very small streams did not support nesting dippers (see also Results).

METHODS

We assessed factors that have been thought to limit the dipper's distribution and abundance (e.g., Kingery 1996). To this end, we estimated stream flow, as an index of potential foraging space, measured characteristics of territories around known nest sites, sampled densities of macroinvertebrate prey in known foraging areas, and characterized nest sites. In addition, we monitored annual variation in apparent annual survival of banded birds and territory occupancy, using this information to assess the relative role of nest sites and food in limiting the local population of dippers.

Estimating Stream Flow

Because our sites were not equipped with stream gauges, we characterized streams by size (flow) as estimated by an equation based on watershed area, elevation, and precipitation (Wiley and Curran 2003). We delineated watersheds by using a digital elevation model from the Shuttle Radar Topography Mission (SRTM; Werner 2001) in combination with digital hydrography interpreted by the U.S. Forest Service (2002) from aerial photography. The SRTM's digital elevation model was the source for preliminary watershed boundaries drawn on the basis of predicted surface flow in the direction of maximum slope (Tarboton et al. 1991). These were compared with observed streams in the Forest Service's database. Where we found discrepancies, we adjusted the digital elevation model to fit the flow pattern observed in the Forest Service's database and recalculated watershed boundaries (Werner 2001). The accuracy of the final delineation of watershed boundaries was verified with the Forest Service streams as well as with USGS topographic maps at a scale of 1:63,360. Later, we estimated the area of two additional watersheds visually by extrapolating boundaries with georeferenced aerial photos and topographic maps in an ArcGIS database; these estimates have a wider margin of error than those calculated by the first method. We estimated the average elevation of each watershed by placing a grid over the watershed on a topographic map (scale 1:25,000) and sampling grid squares at each elevation increment according to a random-number table (sample size was proportional to watershed area).

Precipitation data were obtained from maps in Jones and Fahl (1994). It is important to emphasize that each of these variables is only an estimate, so the estimate of stream flow is rough. Precipitation is the variable with the least detail and the greatest potential source of error because there are

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relatively few gauges measuring the great local variation of precipitation in the mountainous terrain around Juneau and the data available do not include the most recent years. In addition, use of the average elevation fails to reflect marked (but unrecorded) altitudinal differences in precipitation. Our index of stream flow was the 90% exceedance equation for the summer season, meaning that stream flow would exceed the calculated value 90% of the time. Use of the 90% exceedance equation seemed appropriate in view of our initial impression that some streams were “too small” to support nesting dippers. The estimates from other exceedance equations (e.g., 50%) were correlated with the one we chose, so our choice of 90% should not affect interpretation of results.

Dipper Territories and Nest Sites

We surveyed local streams for nesting activity of dippers between 05:00 and 20:00 from late April through early August, 2004–2008, with some preliminary data from 2003. Initially, we surveyed each stream at least three times each season, from tidewater up to a point determined by hiking time on the nearest trail (see below). Surveys in 2004 and 2005 clearly showed that dippers did not nest on certain streams, and these small streams were not surveyed regularly in the following years. We found most nests by following the birds as they carried nest material to a nest site and monitored these sites about twice a week until chicks fledged or the nest failed (Willson and Hocker 2008b). To facilitate frequent monitoring of as many nests as possible, we monitored only nests that were within a 3- or 4-hour round-trip hike of a road. A catalog of all nest locations, resident pairs, and nest success has been placed in the library of the University of Alaska-Southeast, Juneau. Because we surveyed each stream for 5 or 6 years, we knew not only the nest sites used each year but also the distribution of territories along the stream. Therefore, by comparing the distribution of territories among years, we could determine if a given territory was occupied in a given year.

Dippers typically place their domed nests in protected sites very close to the streams where they forage (e.g., Kingery 1996). We characterized nest sites used each year by nesting substrate and our estimates of levels of protection. Each nest site was ranked in one of four levels (from 0 to 3) in four categories: estimated protection from flood (giving the highest rank to nests at a height of at least 2 m above usual summer water levels), weather (presence and completeness of overhang above nest), terrestrial predators (inaccessibility to mink, weasels, squirrels, etc., climbing along extended ledges or over boulders), and aerial predators (inaccessibility and lack of perch sites for ravens, etc.). These estimates cannot account for the effects of extreme events such as rare massive floods and landslides. Ranks in the four categories were summed for an overall estimate of level of protection (maximum = 12).

We also measured several features of the core of each territory at 50-m intervals along a 400-m reach centered on the nest site in 2004, 2005, and 2006 for five intervals per territory. These features included stream substrate (visually estimated proportion of substrate occupied by bedrock, boulders (diameter >25 cm); cobbles (5–25 cm), gravel (2 mm–5 cm), sand, or mud, channel width (measured with tape or range finder), and gradient. Coarse

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substrates harbor more benthic macroinvertebrates than fine substrates (see Willson and Hocker 2008a). Categories of gradient followed those of the Environment and Natural Resources Institute (ENRI), University of Alaska-Anchorage (Major and Barbour 2001), which uses the English system, here converted to the metric system: high, >122 cm in 15 m (>4-foot rise in 50 feet); medium, 30–122 cm in 15 m (1–4-foot rise in 50 feet); low, <30 cm in 15 m (<1 foot rise in 50 feet). We assessed gradients by measuring 15 m (50 feet) along the stream and sighting horizontally from the upper end of the section to the lower; the distance between the water surface and the intersection of the horizontal line of sight with a vertical object at the lower end of the 15-m section gave the amount of rise.

We also recorded type of forest canopy (coniferous or deciduous) and degree of canopy closure over the stream (ranking the width of the canopy opening above each of the five points sampled in a territory core) because previous studies documented effects of these variables on stream invertebrates (e.g., Hawkins et al. 1982, Allen et al. 2003, Kelly et al. 2003). We do not discuss this information further, however, because it proved relatively uninformative: territory cores were distributed quite evenly over the full range of both canopy type and closure categories; the sole exception was a lack of territories on small streams where canopies were fully closed.

During the nesting season in 2004 and 2005 we sampled benthic macroinvertebrates in the riffles of a number of stream reaches, both occupied ($n = 21$, at various elevations in 14 watersheds) and unoccupied ($n = 10$, all at low elevation) by dippers. In occupied streams we took samples in reaches known to be used by foraging dippers and accessible to us; in small, unoccupied streams we took samples in downstream reaches, where stream flow was as high as possible, to minimize the effect of stream size. Sampling took place in May (early in the nesting cycle) in 2004 and in June and July (when many pairs were feeding chicks) in 2004 and 2005. Sampling methods were based on those of ENRI (Major and Barbour 2001). Each sample consisted of five subsamples in units about 46 cm square, spread over at least 25 m of stream, and pooled. We disturbed the substrate manually to a depth of about 5 cm and brushed rocks to dislodge invertebrates, which were swept by the current into the kick-net downstream. Macroinvertebrates (≥ 4 mm in length) were counted and identified at least to family. Densities are presented as numbers per sample. Dippers also pick drifting invertebrates from the water column and water surface (pers. obs.), but these potential prey items were not sampled. At the same time we sampled macroinvertebrates, we also measured the pH and temperature of the water.

Survival Analysis

We banded adult dippers with one USFWS aluminum band and three colored plastic bands for identification of individuals. Birds were caught in mist nets placed across the stream while the adults were feeding chicks. Captured birds were banded, weighed, and sexed by presence or absence of a brood patch (developed by females only). All birds were released on site after being banded. Estimated apparent annual survival was based on resighting of banded adults the following year. This is, necessarily, “apparent” survival because we do not know the frequency of emigration from the study area,

but the observed fidelity of breeding dippers to a site and watershed implies that emigration was low.

We fit a series of Cormack–Jolley–Seber mark–resight models (Williams et al. 2001) to the observations of dippers. These models estimated annual survival (ϕ) and detection probabilities (p); ϕ is the probability that a bird alive and in the study area in one year is still alive and in the study area the following year, and p is the probability that a bird alive and in the study area during a year is detected during the surveys in that year. All marked birds were adults of unknown age ($n = 113$), so estimates apply to adults but are not age-specific. Because we suspected that survival might be a function of winter weather, we used the number of days with temperatures $\leq -12^\circ\text{C}$ as an index of weather conditions, a criterion chosen arbitrarily ($-12^\circ\text{C} \approx 10^\circ\text{F}$; local weather stations record temperature in Fahrenheit). Such cold days were numerous in months with average temperatures $< 1^\circ\text{C}$, a criterion applicable to the White-throated Dipper (*C. cinclus*) of Eurasia (Loison et al. 2002, Sæther et al. 2000; see Willson and Hocker 2008a). Temperatures were available from multiple local sources, all near sea level (see Willson and Hocker 2008a); when sources differed in the number of cold days, we used the minimum plus 0.5 (i.e., ≥ 10 days became 10.5). Because only one marked bird (female) had a gap in its sighting history (i.e., resighted after having been unobserved for ≥ 1 year), we assumed that the probability of birds being resighted did not vary by year or sex [i.e., $p(\cdot)$]. Initially, we fit a model that allowed survival probability to vary by year and sex, including sex-specific effects of the number of cold days (i.e., separate survival estimates for each year for each sex with weather affecting the sexes differently). After fitting the initial model, we fit simpler models that pooled survival estimates by sex or year or excluded the effect of number of cold days. We evaluated the fit of our most general model [$\phi(\text{year} \times \text{sex} + \text{cold days} \times \text{sex})$, $p(\cdot)$] (i.e., we estimated an overdispersion factor \hat{c} ; Burnham and Anderson 2002) by using the median \hat{c} goodness-of-fit procedure in the program MARK (version 5.1). We compared models by using the change (Δ) in the small-sample version of Akaike's information criterion adjusted for lack of fit (i.e., QAIC_c) (Burnham and Anderson 2002), which we used to estimate each model's weight, a measure of support for each model relative to the other models considered.

RESULTS

Streamflow and Occurrence of Nesting Dippers

Dippers occupied territories on many of the streams in our study area (Figure 1). However, nesting dippers were not observed on streams with an estimated summer low-flow exceedance of less than about 0.4 cubic feet per second ($n = 10$; Figure 2), even though several of these streams had cliffs and boulders seemingly suitable for dipper nests (as judged from known nest sites). One of these small streams had been used for nesting at least once in the past.

Seven of 10 streams with exceedances between 0.4 and 0.99 cubic feet per second were usually occupied during this study, two were not occupied,

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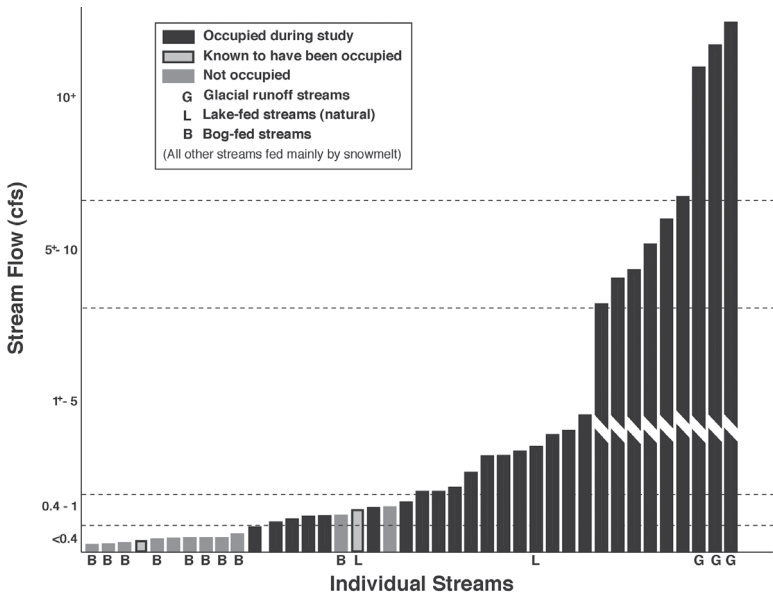


Figure 2. Streamflow (90% exceedance estimates in cubic feet per second, cfs) and occupancy by nesting dippers. Heights of vertical bars indicate streamflow, and streams are arranged on the x axis from smallest to largest. Streams originating in muskeg bogs (B), glaciers (G), or lakes (L) are indicated; all others originate in alpine zones.

and one was occupied once in the recent past (Figure 2). Dippers nested on all monitored streams with exceedance ≥ 1 cubic foot per second ($n = 20$) in at least two of the five years of our study. Nesting dippers were not found on any streams originating in muskeg bogs, including one of apparently suitable size. All three streams of glacial origin had nesting dippers, and all fledged young successfully in at least some years during this study.

Stream reaches occupied by nesting dippers had higher densities of benthic macroinvertebrates (mostly Ephemeroptera, Trichoptera, and Plecoptera in all samples) than unoccupied streams (Wilcoxon rank-sum test, normal approximation, June and July 2004 and 2005, score = 2.7, $P = 0.0067$; May 2004, score = 2.1, $P = 0.016$), but densities of macroinvertebrates in samples from many occupied reaches of streams were similar to those in unoccupied streams (Figure 3).

Territory and Nest-Site Characteristics

The width of the stream channel in the core of 52 dipper territories averaged from 2 m to >16 m. Most territory cores were located on medium- to high-gradient reaches whose substrates were chiefly bedrock and boulders or cobbles (Table 1).

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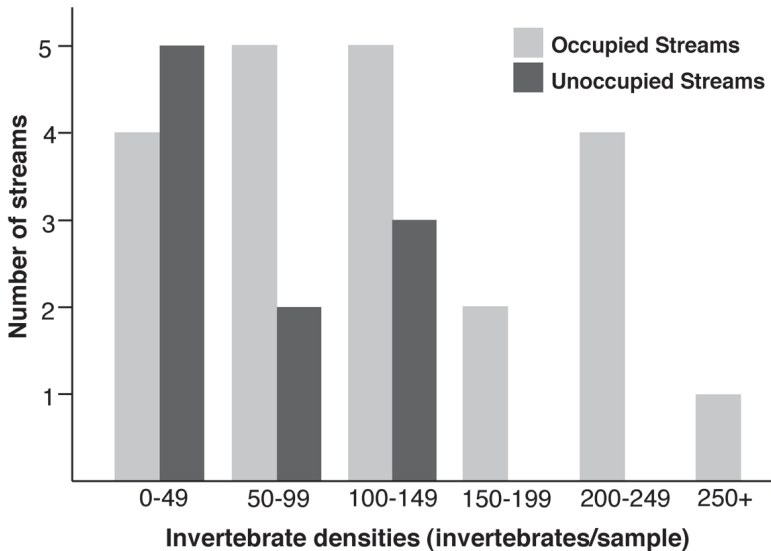


Figure 3. Density of macroinvertebrate prey per sample in reaches of streams occupied and unoccupied by the American Dipper near Juneau, Alaska.

Of 64 nest sites used in at least one year, 58% were on rocky cliffs, 19% were in cavities in boulder piles, 6% were in old wooden dams, 6% were on bridges, and the remainder were in other categories (i.e., a log on a retaining wall, boulder top, steep shale slope, tree-root cavity, concrete spillway). Eleven sites (17%) were anthropogenic in origin.

By our estimates, 75% of nest sites had a high overall degree of protection, with a combined score of at least 10 (of a possible 12). Four nest sites (6%) had little protection from weather, and six sites (9%) had little protection from aerial predators (Table 2). Ten sites (16%) were at some risk of flood, and nine (14%) had little protection from terrestrial predators. Despite the potential risk, most of these nests were probably successful (Table 3; see also Willson and Hocker 2008b). One site on the top of a boulder was exposed to all potential dangers but fledged two broods in 2005.

Annual Variation in Distribution and Abundance

American Dippers nested on up to 21 of the 33 streams we surveyed intensively, depending on the year. Sometimes we found vacant territories on stream reaches that had been occupied in previous years or were occupied in subsequent years. For 31 territories for which we have at least four seasons of data, the frequency of vacant territories was 13% in 2004, 19% in 2005 and 2006, but 48% in 2007 and 32% in 2008 (Table 3); in 2003, 11% of known territories ($n = 19$) were unoccupied.

The rate of vacancy was greatest after three years of low apparent annual survival (from one nesting season to the next) of banded adults (2005–2006,

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Table 1 Characteristics of Streams along 400 m Centered on Known Nest Sites^a of the American Dipper near Juneau, Alaska

Characteristic	n	%
Channel width ^b		
2–6 m	19	37
6–10 m	14	26
>10 m	19	37
Stream substrate ^c		
Bedrock and boulders	32	62
Cobble	16	31
Sand and silt	4	7
Gradient ^c		
High	29	56
Medium	16	31
Low	7	13

^an = 52.

^bCategories are arbitrary.

^cCategories defined under Methods.

2006–2007, 2007–2008) and one season of lower nest success (Table 3). Although apparent adult survival was low in the winter of 2005–2006, nest success the previous season was high (Table 3), so territory vacancy was relatively low. The winter of 2006–2007 had low adult survival and was preceded by a season of low nest success, and territory vacancy in 2007 was high. The winter of 2007–2008 had low adult survival; it was preceded by a year of relatively good nest success but few breeding pairs, so recruitment was low and in 2008 many territories were vacant. Several small streams previously used for nesting had no nesting dippers at all in 2007 and 2008.

We found strong evidence for annual variation in survival rates; the only model that did not allow survival to vary by year but only by sex had a weight of <0.01 (Table 4). The best model, with ~2.7 times the support of the

Table 2 Numbers of American Dipper Nest Sites^a at Four Estimated Levels of Protection from Four Risk Factors

Risk factor ^b	Estimated level of protection			
	High	Medium	Low	None
Weather	52	8	2	2
Flood	35	19	10	0
Aerial predators	50	8	4	2
Terrestrial predators	35	20	8	1

^an = 64.

^bRanked from zero to high and summed for a combined estimate.

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Table 3 Vacancy of American Dipper Territories near Juneau, Alaska, in Relation to Survival over the Previous Winter and Nest Success

Breeding season	Apparent annual survival from previous year (<i>n</i>) ^a	Probable nest success ^b	Vacant territories (<i>n</i>) ^c
2004	67% (12)	91%	13% (19)
2005	53% (40)	94%	19% (31)
2006	39% (56) ^d	74%	19% (31)
2007	37% (57) ^d	92%	48% (31)
2008	42% (19) ^d	—	32% (31)

^a*n* = number of banded birds alive the previous year.

^bPercent of nests fledging chicks, from Willson and Hocker (2008b).

^c*n* = number of territories whose occupancy was determined.

^dSurvival following very cold winters

next best model (Table 4), estimated that survival declined as a function of the number of cold (≤ -12 °C) days (Figure 4); this relationship was almost linear within the range of winters we observed and had a common pattern for both sexes. The second-best model estimated separate, parallel (on the logit scale) slopes for each sex; the third-best model had separate slopes for each sex. The estimated relationship between annual survival and the number of cold days is $\phi = e^{1.396 - 0.0948x} / (1 + e^{1.396 - 0.0948x})$, where *x* is the number of cold days. The estimates (values of ϕ) range from 0.654 (95% confidence interval 0.501–0.781) for years with 8 cold days to 0.324 (95%

Table 4 Statistics for Selection among the Cormack–Jolley–Seber Models Fit to the Mark–Resighting Data for the American Dipper near Juneau, Alaska

Model ^a	Parameters	Δ QAIC _c ^b	Model weight ^c
$\phi(\text{days}), p(.)$	3	0.00	0.610
$\phi(\text{days} + \text{sex}), p(.)$	4	1.98	0.227
$\phi(\text{days} \times \text{sex}), p(.)$	5	4.03	0.081
$\phi(\text{year}), p(.)$	6	4.89	0.053
$\phi(\text{year} + \text{sex}), p(.)$	7	6.94	0.019
$\phi(\text{sex}), p(.)$	3	8.93	0.007
$\phi(\text{year} + \text{sex} + \text{days} \times \text{sex}), p(.)$	9	11.27	0.002
$\phi(\text{year} \times \text{sex}), p(.)$	11	15.13	0.000
$\phi(\text{year} \times \text{sex} + \text{days} \times \text{sex}), p(.)$	13	19.71	0.000

^a ϕ = survival probability; *p* = probability of a dipper being resighted; (days) indicates that the number of days < -12 °C is a factor in the model, (year) indicates that variation in survival by year is a factor in the model; (sex) or (+ sex) or (\times sex) indicates that variation by sex is a factor in the model; (.) indicates the parameter is constant across years and sexes. Statistics are based on $\hat{c} = 1.25$.

^bChange in QAIC_c (a measure of model fit) among models.

^cRelative support for a model relative to other models considered (sum to 1).

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confidence interval 0.222–0.446) for years with 22.5 cold days (Figure 4). Model-averaged (Burnham and Anderson 2002) estimates were very similar to those produced by the best model (Figure 4). The estimated detection probability for both the best model and from model averaging was 0.939 (95% confidence interval 0.758–0.987).

During the years of this study, 61 (54%) of the 113 banded birds nested in only one year and 28 (25%) nested in two years. Only 24 (21%) nested in at least three years.

DISCUSSION

Dippers typically concentrate their activity on fast, clear mountain streams, often on reaches of relatively high gradient, constrained by steep walls (e.g., Kingery 1996, Loegering and Anthony 1999). However, we found some nesting territories centered on reaches of low gradient and fine substrates where anthropogenic structures provided nest sites. Dippers were able to nest along glacial streams, probably because they nested early, before the heaviest loads of sediment came down, and they commonly foraged in nearby tributaries and sloughs with clear water.

All reaches of the streams we studied run through forested terrain, precluding a comparison with the finding of Loegering and Anthony (1999) of the dipper's apparent preference in Oregon for streams through forest over those through other habitats. From observations in Alaska and the Yukon Territory outside our study area (Darcie Neff, Auke Bay Laboratory, Juneau, pers. comm.; Willson pers. obs.), we do not think that American Dippers avoid unforested landscapes in our region.

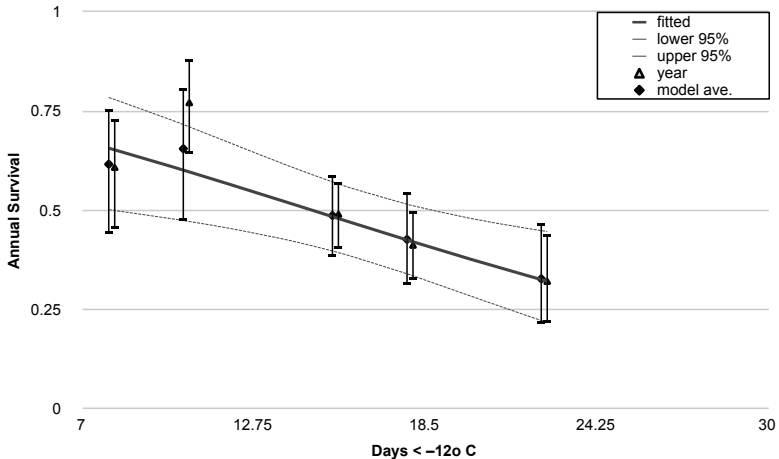


Figure 4. The estimated relationship between probability of annual survival of dippers and the number of cold days ($\leq -12^{\circ}\text{C}$) that year. Dashed lines indicate the 95% confidence interval. Triangles are separate yearly survival estimates from model [$\phi(\text{year}), p(\cdot)$], and diamonds are the model-averaged yearly estimates (Burnham and Anderson 2002).

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Many small streams in our study area originate in muskeg bogs at mid to low elevations but were unoccupied by dippers, despite the occurrence of apparently suitable nest sites on some of these streams. Possible explanations for the lack of nesting dippers on streams originating from bogs might include the lack of prolonged input of snow melt from high elevations and characteristics of the streams' chemistry (David D'Amore, Richard T. Edwards, Forestry Sciences Lab, Juneau, pers. comm.). Although acidification of streams in Britain has led to low density of dippers and their prey (e.g., Tyler and Ormerod 1994), all of the streams we sampled, with pH between 5 and 6, are at least as acidic as acidified streams in Britain. Perhaps the aquatic invertebrates in western North American streams are better adapted to low pH than the European species. We cannot determine if the density and reproductive success of American Dippers (and their prey) are lower than they would if our streams were less acidic; a comparison with streams in Alaskan karst landscapes might be informative.

The broad overlap between occupied and unoccupied reaches in density of macroinvertebrates suggests that (over the observed range) macroinvertebrate density alone did not determine dipper occupancy. Larger (wider) streams, however, typically have more substrate to support benthic invertebrates, so the total abundance of invertebrates should be greater in the larger streams that nesting dippers are more likely to occupy. Thus, the disparity between occupied and unoccupied streams in total abundance of macroinvertebrates is probably greater than the differences in invertebrate density we observed.

The levels of annual survival of adult dippers we estimated include values slightly higher and lower than for other nonmigratory species of similar body size summarized by Martin and Li (1992) and Martin (1995), for the American Dipper as reported in other studies (39–56%; Ealey 1977, Price and Bock 1983), and for the White-throated Dipper (Marzolin 2002). The apparent annual survival we recorded is probably close to the actual value because we seldom missed resighting banded birds that were actually present in the study area (only one banded bird known to be alive after two years was not resighted in the intervening year; detection probability = 0.939). Our regular surveys of numerous streams should have revealed banded birds if they changed watersheds within our broad study area. We found several birds that had shifted territories within watersheds but none that changed watersheds (but see Osborn 2000), although dippers commonly move among watersheds in winter (Willson and Hocker 2008a). It remains possible, however, that some birds moved to regions outside our study area.

Limits to Abundance and Distribution

Several factors may limit dipper abundance and distribution in an area. Nest sites are often thought to be the most important limiting factor, with some influence of prey availability (e.g., Kingery 1996). Evidence of nest-site limitation comes from rapid occupation of new sites such as bridges and nest boxes (Loegering and Anthony 2006, Osborn 1999) and lack of occupation after removal of nest sites (Backlund 1998). There is also evidence, however, for the importance of prey. Campbell et al. (1997) stated that critical habitat is a food-rich stream, although nest sites help determine density

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along a stream. Price and Bock (1983) found territory size to be related to food density. Miller and Ralph (2005) found a higher density of nesting dippers on larger streams (third- and fourth-order) and a lower density on first-order streams. Stream size and susceptibility to drought affect stream use by the White-throated Dipper (Marzolin 2002). In Britain, studies of the White-throated Dipper on acidified streams with reduced abundance of prey support the importance of food availability. Osborn (1999) noted that good but unoccupied nest sites can be found on streams whose quality has been impaired by human activity. The relatively recent decline of dipper populations in the Black Hills of South Dakota has been attributed to a combination of pollution, sedimentation, heavy grazing, dams, dewatering, and modern bridges without nest ledges (Backlund 1998, 2004). In addition, territorial aggression can limit the number of breeding pairs on a stream (Sullivan 1973, Ealey 1977, Price and Bock 1983).

In our study area, evidence that the availability of nest sites limits dipper populations includes the few territories centered on low-gradient streams where suitable nest sites have been provided by man-made structures, such as dams or bridges. These sites had sandy or silty substrates that dippers commonly avoid (e.g., Osborn 1999) because invertebrate prey is more abundant on coarse substrates (e.g., Willson and Hocker 2002a). Presumably, the dippers nesting in these sites needed to forage most intensively at some distance from the nest. During our study, dippers nested successfully in anthropogenic sites, and in general nest success has not been associated with particular habitat features (e.g., Loegering and Anthony 2006, Willson and Hocker 2008b).

The probable importance of prey abundance to the dipper's distribution in our area is indicated by the birds' nesting consistently along larger streams, occasionally along intermediate-sized streams, and not along small streams, despite the existence of seemingly good nest sites. In 1977, however, after several years of unusually high snowfall (Juneau Forecast Office, <http://pajk.arh.noaa.gov>), Robert H. Armstrong (pers. comm.) recorded very young dipper fledglings on a stream categorized here as low-flow. During our study, territorial aggression was observed to eliminate one breeding pair (Willson and Hocker 2008b). Moreover, territorial behavior clearly limited the size of the territory of another pair that foraged widely over two previously occupied but now vacant territories. These three factors taken together, an upper limit to dipper abundance and distribution in our area may be set by stream size (and inferred prey abundance) and nest sites, modified by territorial aggression.

Low overwinter survival, however, especially when combined with poor nest success, reduced density below that upper bound. Apparent annual survival of marked adults varied from year to year, and low annual survival resulted in vacant territories and unoccupied streams. The existence of territories vacant in some years but occupied previously or subsequently, often with good nest success, suggests that sometimes there were too few birds to occupy all the territories.

Even though dippers have dense insulating plumage and are able to function well at very low temperatures (references in Kingery 1996, Willson and Hocker 2008a), cold winter weather appears to reduce their winter survival,

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restricting the number of available breeders (Sullivan 1973, Price and Bock 1983). Nocturnal drainage of cold air down narrow ravines (see Pypker et al. 2007) and the high winds common around Juneau may exacerbate the effects of low temperature. Low nest success in the cold, wet summer of 2006 (Willson and Hocker 2008b) probably contributed to the decline in abundance in 2007.

Weather is also known to affect populations of the White-throated Dipper. For example, populations of this species in France fluctuated in response to flood and drought (Marzolin 2002). Furthermore, low winter temperatures contribute significantly to low overwinter survival of many birds (e.g., Nilsson 1987, Arcese et al. 1992, Robinson et al. 2007, Flockhart and Wiebe 2008), including the White-throated Dipper (Sæther et al. 2000, Loison et al. 2002; see also Tufto et al. 2000).

The American Dipper as an Indicator Species

Southeast Alaska is subject to natural and anthropogenic disturbances that affect the quality of stream water (e.g., Swanson et al. 1998), so the dipper could be useful here as an indicator species for stream quality. Many local streams that can support nesting dippers, however, are so small that only one pair has been found to nest along them, so the absence of a single pair from a small stream would not be valid evidence of impaired stream quality. Low overwinter survival, as we observed, could also be the cause. Using dipper distribution and abundance as an indicator of stream quality necessitates a multi-year, regional assessment of the population rather than simple before-and-after surveys of a single stream subject to suspected disturbance. Annual variation in overwinter survival (and nest success) has too great an effect on distribution and abundance.

Therefore we suggest that a more direct way of using dippers as indicators, in our area, is to assess the birds' physiological and reproductive condition. Studies of the White-throated Dipper have documented many effects of pollution, suggesting many possible responses that could be investigated in the American Dipper. The White-throated Dipper accumulates toxins, lives at lower densities, and eventually abandons streams polluted with sewage, industrial and agricultural waste products, and heavy metals draining from mines in several regions of Europe (Mönig 1985, Tyler and Ormerod 1994, Sorace et al. 2002). Stream acidification from industrial emissions and plantations of conifers in Britain and other parts of Europe has had numerous detrimental effects on dippers there, including poor body condition, later egg-laying dates, decreased eggshell thickness and egg mass, smaller clutches and broods, increased time spent foraging, lower rates of food delivery to chicks, lower rates of energy gain, slower nestling growth, lower chick weights and survival, decreased frequency of second clutches, and ultimately lower population density (Ormerod et al. 1985, 1988, 1991, Ormerod and Tyler 1987, 1990, 1996, O'Halloran et al. 1990, Vickery 1991, 1992, Logie 1995, Logie et al. 1996, Sorace et al. 2002). Many of these effects were induced by changes in the abundance and taxonomic composition of prey (e.g., Ormerod et al. 1985, 1988, Ormerod and Tyler 1991, Vickery 1991). Among other things, changes in the principal prey types resulted in lowered calcium intake (Ormerod and Tyler 1986, Ormerod et al. 1988,

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1991). There is growing evidence for several species of passerines, including dippers, that calcium can be a limiting factor (see Ormerod et al. 1991, Obermeyer et al. 2006).

The effects of pollution and sedimentation on the American Dippers have been studied less than for the Eurasian species. Price and Bock (1983) reported that a heavy input of sediment into a stream led to reduced density and reproductive success of the American Dipper. Feck and Hall (2004) found that dipper density decreased with decreasing abundance of favored prey insects but was only weakly related to several indices of stream quality.

Cyanide in mine-tailing ponds has been lethal to many kinds of aquatic birds (Henny et al. 1994) and could pose a threat to dippers, including during the nonbreeding season, when dippers forage in many kinds of aquatic habitats (Willson and Hocker 2008a). Furthermore, mercury from mine tailings has detrimental effects on fish-eating birds (Henny et al. 2002), and in our area dippers commonly eat fish (Obermeyer et al. 2006, Willson and Hocker 2008b). American Dippers are known to accumulate organochlorines, polychlorinated biphenyls, and heavy metals (including mercury) in eggs and chicks (Blus et al. 1995, Strom et al. 2002, Morrissey et al. 2004), though Henny et al. (2005) detected no effects of these contaminants on the dipper's reproductive success. Exposure to lead decreases the activity of an enzyme essential for formation of hemoglobin and cytochromes (Blus et al. 1995, Strom et al. 2002) and can lead to decreased hematocrit and hemoglobin. Strom et al. (2002) found that decreased activity of this enzyme is associated with higher lead concentrations in the blood of adult and nestling dippers, but they did not assess the birds' survival and reproductive success. For a small, active bird, any decrease in hemoglobin and cytochrome is likely to diminish its metabolic capacity and reduce its ability to deal with high demands for energy. The ability of the American Dipper to cope with heavy metals and other pollutants should be examined more thoroughly to assess at what level and under what conditions particular pollutants have negative effects

ACKNOWLEDGMENTS

The Alaska Department of Fish and Game nongame program funded much of our field work from 2004 to 2008. We thank Dave Albert, The Nature Conservancy, for the majority of the estimates of watershed area and Eran Hood, University of Alaska-Southeast, for instruction on estimating stream flow. Dan Bogan, ENRI at the University of Alaska-Anchorage, instructed us on sampling of benthic insects in streams, and he generously lent equipment. Jamie Womble helped kick-start this program, and John Hudson helped with identification of benthic insects. Several field assistants hiked many miles, waded mountain streams or bushwhacked along them, and provided netting and banding expertise. Cheryl Cook captained the skiff used for the broader survey. Librarians at the University of Alaska-Southeast provided invaluable assistance. Thanks to Steve Matsuoka and an anonymous reviewer for constructive comments. We are also grateful to Maggie Hocker for moral support.

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Accepted 3 March 2009



American Dipper

Sketch by George C. West