**Charles R. Brown**

My research centers broadly on the behavioral and disease ecology of birds, with a specific emphasis on (1) the evolution of social behavior and (2) how arboviruses affect the ecology of birds. Most of my work has been with a single population of cliff swallows (Petrochelidon pyrrhonota), highly social birds that breed in large colonies throughout most of western North America. My long-term project (currently 27 years) at a field site in western Nebraska is among the longest running, continuous field studies on birds in North America, and the number of individuals marked (currently over 187,000 swallows) is the largest of any mark-recapture study of birds in the world.   
  
The cliff swallow project has sought to identify the causes of group living and to understand why breeding colonies vary in size. This has required measuring the costs and benefits of coloniality, which remains one of my major research emphases. My coworkers and I have investigated many of the major questions in behavioral ecology with cliff swallows, and we have used a variety of approaches. Our swallow work has included classical behavioral ecology observations and experiments, a large-scale mark-recapture project and associated demographic analyses, quantitative-genetic estimates of the heritability of behavioral traits, field endocrinological research on hormone levels, studies of selection, and analyses of alternative reproductive tactics including parentage studies. More recently, we have been studying how an RNA arbovirus, Buggy Creek virus (Togaviridae), affects the ecology of cliff swallows and house sparrows (Passer domesticus) that are associated with swallow colonies. Thus, while I work primarily on cliff swallows, my research is conceptually broad.

*Education and Degrees Earned*

* Ph.D., Biology, Princeton University, 1985
* B.A., Biology, Austin College, 1981

*Areas of Research Focus*

* Behavioral Ecology
* Ornithology
* Disease Ecology

*Previous Teaching Experience*

* 1985–1989, Assistant professor of biology, Yale University
* 1988–1989, Visiting scholar, Department of Zoology, University of Washington
* 1989–1993, Associate professor of biology with term, Yale University
* 2001 (summer), Visiting associate professor, University of Nebraska–Lincoln

*Previous Relevant Work Experience*

* 1986–1993, Curator of ornithology, Peabody Museum of Natural History, Yale University

*Professional Affiliations*

* American Association for the Advancement of Science
* American Ornithologists’ Union
* Animal Behavior Society
* Association of Field Ornithologists
* British Ornithologists’ Union
* Waterbird Society
* Cooper Ornithological Society
* International Society of Behavioral Ecology
* Wildlife Disease Association
* Wilson Ornithological Society

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**Research Interests:**My research interests center on the evolution of social behavior in vertebrates. I am especially interested in the effect of group size on social behavior. Much of my research focuses on why animals live in colonies. The adaptive significance of group-living in animals has attracted the interest and attention of biologists for decades, and we presently have a relatively clear understanding of the selective pressures that lead to territoriality (economic defensibility) and cooperative or communal breeding (inclusive fitness and habitat limitation) in vertebrates. My National Science Foundation-funded long-term research focuses on a colonially nesting bird, the cliff swallow (Petrochelidon pyrrhonota), which I have been studying at a field site in Nebraska for the last 21 years.  
  
**There are four major aspects to my research program:**  
  
**(1)**Measurement of the socio-ecological costs and benefits of coloniality (e.g., predator avoidance, ectoparasitism, enhanced food-finding) as a function of group size.  
  
**(2)**Evaluation of the alternative reproductive options (e.g., conspecific brood parasitism, extra-pair copulations) that become available to animals once they have formed groups.  
  
**(3)**Investigation of the demographic consequences of living in colonies and in particular the effect group size and associated socio-ecological costs and benefits may have on life history parameters. **(4)**Examination of the observed patterns of colony choice by individuals and hypotheses for why group size varies.   
  
Cliff swallows are common throughout much of western North America, building their mud nests in dense colonies underneath rocky overhangs on the sides of cliffs and canyons and also underneath bridges and in highway culverts. My study site is in southwestern Nebraska near the University of Nebraska's Cedar Point Biological Station. In this area cliff swallows breed in colonies ranging in size from 2 to 3700 nests, plus solitarily, making this population ideal for investigating the effects of group size.  
  
**(1) The socio-ecological costs and benefits of coloniality**  
  
Over the years I have examined a variety of potential costs and benefits of cliff swallow coloniality and how they vary with group size. This was a major focus of my research program in the early years of studying cliff swallows, and continues to date. These results are described fully in my book, Coloniality in the Cliff Swallow. Below I highlight two of the more interesting aspects of this work, some of the novel findings, and the related work planned or in progress.  
  
**Foraging strategies.**--Cliff swallow colonies function as "information centers" in which individuals unsuccessful at finding food locate other individuals that have found food and follow them to a food source. Many people had searched for information centers in various species of birds and mammals since the early 1970's, but I was the first to document their existence in any bird (Science 234: 83-85, 1986). Advantages associated with information sharing on the whereabouts of food are substantial and probably represent a major reason why cliff swallows live in colonies (Ecology 69: 602-613, 1988). I also discovered that cliff swallows represent one of the few birds (and indeed non-human vertebrates) that actively communicate the presence of food to others by giving distinct signals (calls) used only in that context (Anim. Behav. 42: 551-564, 1991). The evolution of such information sharing is perplexing, because the typical beneficiaries of calling are individuals unrelated to the caller. Future work is planned to investigate individual differences in foraging efficiency and potential asymmetries among individuals in the benefits gained from information sharing; the degree to which cliff swallows forage in a "risk-sensitive" manner; how foraging-related benefits vary with group size; and how features of the local resource base (that is, differences in prey availability and type) affect information sharing in colonies of different sizes.   
  
**Ectoparasitism.**--Cliff swallows are associated with several blood-sucking ectoparasites, and infestations in the nests of some colonies can be severe. Ectoparasites increase with cliff swallow colony size and severely depress nestling swallow body mass and survivorship (Ecology 67: 1206-1218, 1986). My work demonstrated the most substantial, regularly occurring cost due to parasites for a colonial species yet described. Ectoparasitism undoubtedly represents the most important cost of living in colonies for cliff swallows. Future work will model the spread of ectoparasites within colonies of different sizes and spatial configurations, to predict the degree of within- and between-colony variance in parasite load and how this variance affects the birds' responses. Using the long-term data from my population, I am charting patterns in annual colony site usage to determine if variation in site usage is an adaptive response to parasite build-ups. Studies of ectoparasitism are facilitated by our experimental fumigation of nests in the field, which makes it possible to create parasite-free nests wherever we wish. In collaboration with Bruce Rannala, I have begun to address the population genetics of one of the ectoparasites, the cimicid swallow bug. Populations of these bugs occur in discrete colonies with limited dispersal between colony sites. We have begun to test hypotheses concerning the population structure and differentiation of these bugs using both empirical (field) data and molecular genetic techniques. In collaboration with scientists at the Centers for Disease Control in Fort Collins, Colorado, I have also initiated studies of arbovirus transmission within cliff swallow colonies. The cimicid bug is a vector for western equine encephalitis virus, and presently we are investigating how swallow colony size and density and a colony's spatial position relative to other colonies influence viral transmission using a metapopulation approach. This work has obvious biomedical implications.   
  
**(2) Alternative reproductive options**   
  
Once animals form colonies, opportunity exists for some individuals to exploit others, and these options often do not exist for more solitary animals. Colonial individuals can parasitize the reproductive effort of others by laying eggs in neighbors' nests (conspecific brood parasitism). Males may seek copulations with nearby females to whom they are not paired (extra-pair copulations). With neighboring nests in close proximity, the potential exists to steal mud and nesting material for one's own use, as well as to perhaps decrease the relative fitness of neighbors by destroying one or more of their eggs. My research has investigated all of these potential reproductive options (see book).   
  
Conspecific brood parasitism.-- I was among the first to show (Science 224: 518-519, 1984) that conspecific brood parasitism is a major strategy used by substantial numbers of individuals; up to 43% of cliff swallow nests may have one or more eggs not belonging to the owners. Within the last ten years, behavioral ecologists have recognized the importance of conspecific brood parasitism, and it has now been reported in a variety of bird species. I discovered a new form of brood parasitism previously unknown in birds (Nature 331: 66-68, 1988). Cliff swallows not only lay eggs in other individuals' nests but also physically carry eggs into neighboring nests. This novel behavior expands the time window during which nests may be parasitized, and egg transfer occurs regularly in swallow colonies. I have used protein electrophoresis to study parentage in cliff swallow broods, and the biochemical analyses have suggested that brood parasitism is a major alternative strategy used by these birds. I have also determined that cliff swallows often destroy one or more eggs of their neighbors. Birds furtively enter an unattended neighboring nest and toss out single eggs. These egg tossings are not related to attempts to usurp nests, and as a result their adaptive significance is puzzling.   
  
**(3) The demographic consequences of coloniality**  
  
To fully measure the costs and benefits of coloniality, one must be able to follow individuals throughout their lifetimes and measure lifetime reproductive success. Cliff swallows can live up to at least eleven years, and thus annual measures of reproductive success are potentially misleading, especially if success varies in any way with age, as my data suggest for cliff swallows. One of the major goals in my research thus far has been to mark large numbers of individuals, enabling me to follow the reproductive histories of these birds. By knowing the histories of individuals from year to year, I am able to measure lifetime reproductive success; determine whether an individual's choice of colony size from year to year is stochastic or to any degree predictable; whether kin tend to settle near each other; whether reproductive costs occur in older individuals; the long-term effects of ectoparasites; how reproductive success affects colony site fidelity; the effect of colony size on cohort recruitment into the population; and other questions critical to an understanding of social evolution at the population level.   
  
Since 1982, my assistants and I have marked over 158,000 birds in our study population with permanent bands. Some information is known for each of these individuals, and many have been caught repeatedly in successive years. I am now gathering a huge amount of recovery information each year, and my data set is unique. I know of no comparably sized data set on any North American species that will provide this kind of information.   
  
My long-term mark-recapture program is beginning to yield results. For example, I have found that the extent of ectoparasitism a nestling bird experiences during the short time it is in the nest (21 days) has a major influence on whether that individual disperses to another colony the following spring or returns to its natal site (Ecology 73: 1718-1723, 1992). Ectoparasitism thus appears to determine dispersal, a result not previously known for birds or mammals, and one that has implications for social behavior, population genetic structure, and host-parasite coevolution. I have begun to apply mark-recapture data to address other life-history questions, such as how survival is related to clutch size, laying date, and the tendency to engage in conspecific brood parasitism or extra-pair copulation.   
  
**(4) Why do animals choose colonies the way they do?**  
  
Cliff swallows, like most colonial birds, exhibit substantial variation in colony size. Some individuals nest solitarily, others breed in moderately sized colonies, and still others live in huge colonies of thousands of birds. Colony size variation has not been explained satisfactorily in general or for any single species. My data are now beginning to suggest that birds in certain colony sizes are more successful than birds in other colony sizes, yet extensive size variation persists. I have proposed various hypothesis to explain why birds choose colony sizes in the observed fashion (Trends Ecology Evolution 5: 398-403, 1990), and have begun to examine these hypotheses in cliff swallows.   
  
I have studied movement patterns of cliff swallows upon their return to the study area and before they have chosen a colony in which to breed. Birds are caught and radio transmitters affixed to their backs, and their subsequent movements followed for 7-21 days. Cliff swallows have proven to be easy species to radio-track. Individuals clearly visit many colony sites before settling; they do not automatically settle in the first one they visit or even the first one they find a nest in. They select a colony in many cases days before successfully establishing ownership of a nest. The birds also move extensively between colonies late in the year. These results indicate that the birds obviously assess sites, but the cues they use are still not clear.   
  
I am also using my extensive long-term data set to examine the histories of the birds' colony choices from year to year. Payoffs for colonies of certain sizes may vary with age or condition of the bird, and thus birds should switch between sites as they get older or their condition changes. Cliff swallows move extensively among sites between years, and the patterns will likely tell us much about the advantages and disadvantages of using certain colony sizes and how these differ among birds.   
  
  
**Current work**   
**(1) Completion of the long-term demographic study.** To achieve robust estimates of survival, cohorts must be followed for 3-4 years, and consequently I anticipate continuing to collect some demographic data through 2001. As we compile enough information for analyses of the effect of individual years on survival probabilities, this long-term study will be especially valuable in determining the importance of particular "good" and "bad" years on life history. For example, 1992 was the third coldest summer in Nebraska on record (dating to 1876). Many cliff swallows died, and the demographic consequences may persist for years. In 1996, another severe mortality event caused by bad weather reduced the population by about 50%, and we are now exploring the implications and natural selection that may have resulted from this event (see Evolution 52: 1461-1475, 1998).   
  
**(2) Studies of transmission dynamics of ectoparasites and their associated alphaviruses.** My work to date has indicated that ectoparasitism is complex in cliff swallows, with unpredictable effects on the birds' behavior and life histories. We have only scratched the surface in our understanding of host-parasite coevolution in this system. Future work is planned to investigate, in particular, the between-group and within-group transmission of ectoparasites and their viruses, work that will have direct relevance to epidemiology. This system also provides an ideal model to study genetic differentiation among the parasites themselves. Hemipteran swallow bugs, confined almost exclusively to the cliff swallows' nests in spatially discrete and often isolated colonies, exhibit rather limited dispersal between colonies and often undergo periods of extinction within a site when the birds choose not to occupy it in a particular year. The bugs provide a superlative opportunity to test, with both field data and molecular methods, various equilibrium and non-equilibrium models of genetic differentiation among animals exposed to frequent extinction and occasional recolonization events. I am presently collaborating with others (and plan to continue to do so) whose primary interest is in population genetic questions. We have initiated research to understand the transmission mechanisms that produce the observed increase in parasitism by swallow bugs with cliff swallow group size. Experiments will measure the rate at which bugs immigrate into a colony and the rate at which transient cliff swallows (that introduce bugs) visit different colonies. The results will be among the first attempts to measure between-group transmission of parasites in a social species. The swallow bug also serves as a vector for arthropod-borne alphaviruses (genus Alphavirus) that are closely related to those that cause western equine encephalitis. In cooperation with virologists at the Centers for Disease Control, we are studying the prevalence and transmission dynamics of encephalitis-related alphaviruses in cliff swallow colonies. Preliminary results show several as yet unidentified virus strains isolated from swallow bugs, and we have found an increased incidence of virus in nests in larger colonies. We are studying the transmission cycle and ecology of the viruses associated with cliff swallows and their ectoparasites; this system can provide a model for the study of other Alphavirus involving migratory birds.   
  
**(3) Information centers.** We have only begun to understand the complexities of information sharing in these birds. There is evidence now that some individuals within a cliff swallow colony forage in very different ways than others. How do these foraging strategies lead to the overall patterns of information sharing seen in cliff swallow colonies?   
  
**(4) Comparisons with cave swallows.** I am initiating a comparative study of the related cave swallow (Petrochelidon fulva), which occurs in Central America, Mexico, and the southwestern United States. To date my work has focused almost exclusively on a single species (cliff swallow), but comparisons with the cave swallow are likely to be instructive. For example, cave swallows are intermediate between highly colonial cliff swallows and more solitary barn swallows (Hirundo rustica) in virtually all aspects of their breeding biology and social behavior. Barn swallows live in colonies because their nesting substrates are limited, while cliff swallows clearly do not live in colonies for that reason. Cave swallows may reveal what ecological or social pressures have brought about the transition to a more social life style. Involvement of graduate students in this seems likely.   
  
**(5) Hormonal and immunological correlates of colony size.** In collaboration with others, I have initiated a comparative study of hormone levels among cliff swallows in different sized colonies. A bird's hormone condition may reflect its social environment, with serious consequences for its immunocompetence which in turn may affect its survival and lifetime reproductive success. A bird's hormone levels may also cause it to choose a given colony size. I have also begun a comparative study of immunocompetence among cliff swallows in different sized colonies. Immunocompetence is a measure of condition in birds, and this study should help reveal what sort of individual ("quality") differences occur among birds occupying small versus large colonies. We will also explore the hypothesized connections between hormone levels and immunocompetence.   
  
  
**Teaching:**

* Biol 3153-Animal Behavior
* Biol 3164-Field Ecology
* Biol 3614-Ornithology

**Selected Publications:**

* Brown, C. R., M. B. Brown, S. A. Raouf, L. C. Smith, and J. C. Wingfield. 2005. Effects of endogenous steroid hormone levels on annual survival in cliff swallows. Ecology, in press.
* Smith, L. C., S. A. Raouf, M. B. Brown, J. C. Wingfield, and C. R. Brown. 2005. Testosterone and group size in cliff swallows: testing the “challenge hypothesis” in a colonial bird. Hormones and Behavior 47: 76-82.
* Brown, C. R., and M. B. Brown. 2004. Group size and ectoparasitism affect daily survival probability in a colonial bird. Behavioral Ecology and Sociobiology 56: 498-511.
* Brown, C. R., and M. B. Brown. 2004. Empirical measurement of parasite transmission between groups in a colonial bird. Ecology 85: 1619-1626.
* Brown, C. R., and M. B. Brown. 2003. Testis size increases with colony size in cliff swallows. Behavioral Ecology 14: 569-575.
* Brown, C. R., R. Covas, M. D. Anderson, and M. B. Brown. 2003. Multistate estimates of survival and movement in relation to colony size in the sociable weaver. Behavioral Ecology 14: 463-471.
* Brown, C. R., and M. B. Brown. 2002. Spleen volume varies with colony size and parasite load in a colonial bird. Proceedings of the Royal Society of London B 269: 1367-1373.
* Brown, C. R., N. Komar, S. B. Quick, R. A. Sethi, N. A. Panella, M. B. Brown, and M. Pfeffer. 2001. Arbovirus infection increases with group size. Proceedings of the Royal Society of London B 268: 1833-1840.
* Møller, A. P., S. Merino, C. R. Brown, and R. J. Robertson. 2001. Immune defense and host sociality: a comparative study of swallows and martins. *American Naturalist* 158: 136-145.
* Brown, C. R., and M. B. Brown. 2001. Avian coloniality: progress and problems. Pp. 1-82 in *Current Ornithology*, Vol. 16 (V. Nolan and C. F. Thompson, eds.). Plenum, New York.
* Brown, C. R., and M. B. Brown. 2000. Heritable basis for choice of group size in a colonial bird. Proceedings of the National Academy of Sciences USA 97: 14825-14830.
* Brown, C. R., M. B. Brown, and E. Danchin, 2000. Breeding habitat selection in cliff swallows: the effect of conspecific reproductive success on colony choice. *Journal of Animal Ecology* **69**:133-142.
* Brown, C. R., and M. B. Brown, 2000. Nest spacing in relation to settlement time in colonial cliff swallows. *Animal Behaviour***59**:47-55.
* Brown, C. R., and M. B. Brown, 1999. Natural selection on tail and bill morphology in barn swallows *Hirundo rustica*during severe weather. *Ibis* **141**:652-659.
* Brown, C. R., and M. B. Brown, 1999. Fitness components associated with laying date in the cliff swallow. *Condor***101**:230-245.
* Brown, C. R., and M. B. Brown, 1999. Fitness components associated with clutch size in cliff swallows. *Auk* **116**:467-486.
* Brown, C. R., and M. B. Brown, 1998. Intense natural selection on body size and wing and tail asymmetry in cliff swallows during severe weather. *Evolution* **52**:1461-1475.
* Brown, C. R., and M. B. Brown. 1998. Fitness components associated with alternative reproductive tactics in cliff swallows. *Behavioral Ecology* **9**:158-171.
* Brown, C. R. 1998. *Swallow Summer*. Univ. Nebraska Press, Lincoln, 371 pp.
* Brown, C. R. and M. B. Brown, 1996. *Coloniality in the Cliff Swallow: the Effect of Group Size on Social Behavior*. Univ. Chicago Press, Chicago, 566 pp.
* Brown, C. R. and M. B. Brown, 1988. A new form of reproductive parasitism in cliff swallows. *Nature***331**: 66-68.
* Brown, C. R., l986. Cliff swallow colonies as information centers. *Science* **234**:83-85.
* Brown, C. R. and M. B. Brown, 1986. Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhonota*).*Ecology* **67**:1206-1218.
* Brown, C. R., 1984. Laying eggs in a neighbor's nest: benefit and cost of colonial nesting in swallows. *Science* **224**: 518-519.

**Senior Scientific Staff:**

* Mary Bomberger Brown, Research Associate (M.S., 1982, University of Nebraska-Lincoln)
* Amy Trachte, Research Associate (B.S., 2004, University of Oklahoma).

**Research Students and Products (Current):**

* Bridget Stutchbury (Ph.D., 1990,Yale): Plumage color and reproductive tactics in male purple martins.
* Bruce Rannala (Ph.D., 1995, Yale): Demography and population structure in island populations
* Jeffrey Davis (M. S., 1998): Costs and benefits of coloniality in purple martins.
* Sarah Huhta (M. S., 1999): Reproductive success and coloniality in bank swallows.
* Christine Sas (M. S., 2000): Ecological correlates of colony size in cliff swallows.
* Cheryl Ormston (M. S., 2001): Breeding-site characteristics and range changes of culvert-nesting swallows in Texas.
* Ana Briceno (M.S., 2002): Tail length and sexual selection in the North American barn swallow.
* Heath Weaver (M. S., 2002): The costs and benefits of coloniality in cave swallows.
* Thirty-three undergraduate student research projects since 1985.
* Sixty-five undergraduate research assistants since 1982

**Other Responsibilities:**

* Editor in chief, *Journal of Field Ornithology*
* Associate editor, *Behavioral Ecology and Sociobiology*
* Chair, Undergraduate Committee
* Member, Graduate Committee