

obody expects a penguin to slump onto the ice and squawk brokenly to his buddies, "I shoulda seen it coming. She was always after me about money, see. . . . "

Not many nests are wrecked by credit card excesses, so what does drive birds to divorce? Biologists are scrutinizing bird families, from courtship to breakup, with new interest these days.

For years, scientists assumed that birds which nested together pretty much stayed together without slipping off to visit alluring neighbors. In the 1980s, however, DNA analyses of nestlings revealed that the male who helps tend them is not always their genetic father. "A lot of birds are having a bit on the side," says Jeffrey M. Black of the University of Cambridge in England, "so many theories about evolution and social behavior have been turned on their heads."

From this upset, studies of feathered divorce have begun to emerge. "I think you're going to see a lot more," Black predicts.

Many researchers use the term "divorce" for paired birds that separate or fail to reunite during the next breeding opportu-

nity. When the word first showed up in ornithology papers, "there was an uproar," Black remembers. However, ornithologists didn't seem to take to such proposed alternatives as "severance," "breakage," "dissolution," or that masterpiece of neutrality, "nonretainment." In *Partnerships in Birds* (Oxford University Press, 1996), which Black edited, he observes that "no sane reader should misinterpret divorce in birds as implying legal dissolution of a marriage, with alimony and lawyers' fees."

nly a minority of animals divorce—because only a few form pair bonds in the first place. These pair-bonding oddities include only about 5 percent of mammals, estimates T.H. Clutton-Brock of Cambridge. Gibbons, jackals, marmosets, and certain mice appear to mate for life.

A few invertebrates, such as burying beetles, also make a lasting commitment. The male starfish-eating shrimp guards its chosen female from the attentions of other males. A desert spider (*Agelenopsis aperta*) takes a lifelong mate, although they live only about 49 days.

More than 9,000 bird species pair up

with a mate for certain times and purposes, says Black. Persistent partnerships have evolved in fewer species, including very old and more modern ones.

Black has collected estimates of divorce rates in more than 100 species of birds. The percentage of pair bonds that break ranges from nearly 100, in house martins and greater flamingos, to roughly zero in Australian ravens and the waved albatross. Humans, who divorce in 40 to 50 percent of new marriages in the United States, fall into the same range as the masked booby.

The new scrutiny has tarnished even that ultimate icon of romance, the swan. André A. Dhondt, a Cornell University ornithologist who contributed to *Partnerships in Birds*, says "the biggest disappointment of the book for a nonornithologist is that swans are not the most faithful of birds." Five percent of whooping swan pairs end in divorce, and as many as 1 in 10 pairs of mute swans split up. However, Bewick's swans almost never separate.

Divorce rates differ not only among species but among different populations of the same species, much as humans in Nevada untie the knot at a higher rate than those in Maine. Dhondt and his col-

MARCH 7, 1998

SCIENCE NEWS, VOL. 153

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Ornithologist Jeffrey Black has collected reports from field studies to determine what percentages of mated bird pairs divorce.

leagues monitored great tits, little birds that nest in cavities, at nine sites in Belgium. Divorce rates ranged from essentially zero to 51 percent.

Dhondt attributes these differences mostly to habitat. Large forest patches seem to promote higher divorce rates. There, birds gather in big flocks during the winter and search for food. At the same time, they get a good look at the mating options, Dhondt suggests. Moreover, mates wintering in these flocks are more likely to get out of synch, leading one member of a pair to start breeding with another bird before the original partner is ready.

In smaller patches of woods with good gleanings or urban habitats with luxurious bird feeders, birds are less likely to form roving flocks. These neighborhoods have lower divorce rates, Dhondt says.

he decisive event in some avian breakups may last only 5 minutes, so the chances that an ornithologist will see it are slim, laments Lewis W. Oring of the University of Nevada, Reno.

Oring himself has managed to wit- In ness several divorces caused by tin home wreckers, who chase one of the mates away. In killdeer, these battles tend to be "subtle," he says. "There's a lot of bluffing and a lot of chasing," with occasional quick jabs to yank out feathers. He's never seen a serious injury.

Spotted sandpiper divorces can get much nastier. These breakups stretch the meaning of divorce, since each thriving female keeps a harem of males on her territory. When another female tries to take over the stable, the resident fights hard, Oring says. He's seen a female puncture a rival's eye or break her leg. During these fights, males "sit and watch the females

duke it out," he says. "It's in the males' best interest to have the best females."

Great skuas, large seabirds not given to subtlety, sometimes kill each other during disputes over a mate, reports Robert W. Furness of the University of Glasgow in Scotland. He has witnessed females making all-out attacks to win another bird's territory and partner. "The unattached female will swoop down with talons out," he says. At first, she may just brush over the resident female, but as the fight escalates, those talons get used.

The male great skua may be out at sea during the fight and come home to find a new mate waiting for him. If the male happens to be on land during the altercation, "he certainly doesn't come rushing to the defense of his partner," Furness observes.

Female birds can sit out a battle just as



In king penguin colonies, where mates spend little time together, divorce rates are high.

coolly, says ornithologist Clive Minton of Melbourne, Australia. He watched a male mute swan attack a resident male and eventually drive him away from his territory, his mate, and four 2-month-old cygnets. After the prolonged battle, the female "sailed off down the stream with the new mate and family as if nothing had happened."

Guys do the home wrecking in species like blue ducks, African black ducks, and song sparrows, reports Bruno J. Ens of the Institute for Forestry and Nature Research in Den Burg, the Netherlands. He,

Black, and Sharmila Choudhury of the Wildfowl and Wetlands Trust in Slimbridge, England, have reviewed field studies of birds with long-standing pair bonds. Among house wrens, the males do most of the invading, although females sometimes try to chase away other females and claim their mates. Oystercatchers are equal-opportunity mate usurpers.

Divorce on the grounds of desertion is even more difficult to observe. Ens and his colleagues report indirect evidence—mated birds who suddenly turned up at new addresses—that blue ducks, ptarmigan, great tits, oystercatchers, and house wrens do indeed desert their homes. In these species, the deserter is usually the female; the male gets the territory.

The frequency of deserting females does not surprise Dhondt, who compares relative investments in reproduction. "There is more at stake for females than males," he points out.

o find out who benefits from a divorce, Dhondt has tallied the number of subsequent off-spring of divorced male and female blue tits. "Typically, females improve their breeding success, but the males don't," he reports.

Female black-capped chickadees tend to dump their mates for males of higher social standing, say Ken Otter of the University of Copenhagen and Laurene M. Ratcliffe of Queen's University at Kingston in Ontario.

Queen's University at Kingston in Ontario. Research on willow tit divorce finds that females ditch their mates for older birds.

Older usually means more desirable in both females and males, says Ens. More mature females generally start breeding earlier, and that extra time frequently boosts the number of fledglings during a season. In many birds, the age of the female seems more important than the age of the male, he notes.

Eventually, older birds may lose their edge in the egg business. Barnacle geese can live some 20 years, but their prime



reproductive years come between ages 6 and 11, says Black. "You want to get a middle-aged partner to really peak."

The singles scene can be tough for some species. Among red-billed gulls in a region with few males, 32 percent of females that lose their mates through death or divorce never breed again. Long-time gull watcher James A. Mills of Corning, N.Y., who reports that number, notes that some of these loners lived 10 more years.

Even birds that do find a new partner may lose valuable breeding time, says Mills. Among the red-billed gulls who eventually found new mates, 41 percent took so long that they missed a breeding season.

In contrast, Cassin's auklets, chunky seabirds that breed on islands or cliff faces, routinely pick up new mates within days of a divorce. Just how isn't clear, says William J. Sydeman of Point Reyes Bird Observatory in Stinson Beach, Calif. As the birds convene to excavate burrows for their eggs, "there's a horrendous chorus of calling and digging," he says. However, courtship has been tough to study, since much family life takes place underground.

Dhondt suggests that too often, researchers focus on the supposed costs of divorce, such as missing a breeding season or having to make do with a less desirable, younger bird. For some species, there may not be a cost. "In tits, there's no evidence that there is," he says.

Male great skuas find divorce expensive, but that could be because the divorcés were losers from the start, says Furness, who notes that divorced males tend to take longer than widowed birds to pair up again. He suggests that males vary greatly in how well they provide food, while "one female seems to be much as good as another" at guarding the young and the territory. "If he doesn't get enough food, then he's a crap male, and she should leave him," Furness advises.

hese observations of skuas contradict the well-established incompatibility hypothesis of avian divorce, Furness argues in the December 1997

ANIMAL BEHAVIOUR. Developed by J.C. Coulson in the 1960s, this theory holds that some birds are incompatible, reproducing poorly when together even though each might thrive with a different mate. Such pairs are more likely to split.

Among the kittiwakes that Coulson studied, one bird of a pair might make quick trips for food, while the other would stay out a long time on this errand. He considered such pairs incompatible. As Furness puts it, "You're sitting there waiting to make your little short trip, and your partner's away for ages."

In contrast, Furness sees divorced male skuas as discards that would not be

very compatible with any females. He proposes that the skua data fit what he calls the "better option hypothesis," the idea that birds divorce because one gets a more appealing offer.

"It's a nifty idea," says Black. Although there hasn't been a lot of evidence for the theory yet, he notes, his studies of barnacle geese have provided some support. In this species, older birds rank as more desirable mates than younger ones. After a large die-off of older birds, which frees up prime mates, the divorce rate increases.

Black has counted at least 11 hypotheses to explain the dynamics of bird divorce. The list includes theories that emphasize the role of habitat and one nicknamed "the keeping company hypothesis."

"If you keep company all year long, you're more likely to stay together for life," Black says. He finds the idea appealing for the geese he studies, which strike him as "traditionalists." Species that stay together for only a few weeks, and must then find each other again the next season, tend to be less loyal.

All of these theories about divorce and mating systems apply only to birds, cautions Furness. "I wouldn't try to draw any conclusions about humans."

Black also declines to comment on nonfeathered pair bonds, but he admits that some of the hypotheses at least sound familiar to the species doing the hypothesizing. "The parallels are endless, aren't they?"

