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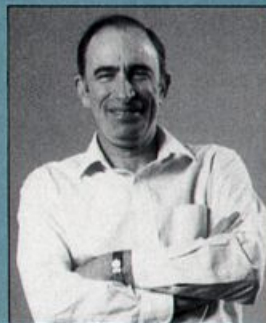
On my ornithology class field trip to the California coast this spring, I lucked out once again. At pescadero there were Caspian Terns standing on the sand along the edge of the inlet and, sure enough, as we watched, an individual came zooming over carrying a fish. The tern landed on the sand and began waving the fish at the other terns. Triumph! I had alerted the class to watch out for "courtship feeding," and there it was going on before their very eyes!

Virtually every year I've taken the class to the coast, the terns have been cooperative. Male terns often try to lure prospective mates into their territories by offering them fishes—it's a form of display. Displays are moves made to signal information to members of the same or other species (calls and songs often accompany displays and signal information, but ornithologists usually limit the term "display" to visual signals). A male tern waving a fish, a male mallard swimming around a female arching his neck and flicking water towards her, or a male widowbird dragging its grotesque tail in undulating flight over the African savanna are all performing courtship displays. The message is simple: "I'm a great catch; let's mate."

A male Gray Catbird fluffs its feathers, spreads and lowers its tail, and raises its wings, and another male catbird gets the signal: "Back off, this

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BIRDING FOR FUN



Displays and Dominance

Illustrations by Darryl Wheye

is my territory." A male Northern Bobwhite fluffing its feathers while holding its body horizontal and spreading its tail is telling another male something like: "I'm dominant over you; accept it or fight." A penguin bowing to its nest-guarding mate and calling as it returns from the seas loaded with krill to regurgitate for their chicks is performing a greeting display. Its message is something like: "Honey, it's okay, it's me." A baby American Dipper gaping and squealing is performing a begging display with the simple message: "Feed me now!"

After the thrill of learning to identify birds has started to fade, many birders discover the fun of watching (and sometimes taking notes on) avian behavior. Displays are some of the most interesting

aspects of that behavior. Not only can they be spectacular, as when male prairie-chickens strut their stuff on a "lek" (a traditional courtship ground), but displays often present the challenge of decoding the message. Sure, for gaping chicks it's easy—but in many cases the meaning of a display is obscure, often depending on the context in which it is given. For instance, that fluffed-up male catbird may indeed be telling another male to stay out of its territory. Then again, it may be trying to persuade a reluctant female that he is a desirable mate. And if he is giving a cat-like call simultaneously, it may

also be distracting a predator, or at least letting the predator know that its presence has been detected.

Male Lapwings, large European shorebirds, have a dazzling flight display. It is a complex sequence that includes a “butterfly flight” (flying slowly with deep wingbeats), a zig-zag flight in which the body is rotated from side to side as a humming noise is produced by the outer primary wing feathers, and a silent flight with shallow wingbeats close to the ground, ending with a steep climb. That routine may be followed by a straight flight accompanied by two songs and the beginning of a third song which finishes during a steep climb that culminates in a vertical dive. One might suppose that such a complex sequence would signal a rather specific message, but in fact males use the same display to signal other males, females, and even an unspecified audience when they return to their territories. At other times, the display is given “spontaneously;” that is, when there is no discernable (to a human observer) stimulus. Obviously, the display must have very different meanings in these different contexts—unless the basic message is: “I’m a healthy male Lapwing; behave appropriately toward me.”

The use of displays by birds can save them a great deal of trouble. Many years ago, the curiosity of Norwegian behaviorist, Thorleif Schjelderup-Ebbe, was aroused by the lack of fighting over chick feed in flocks of hens. He did some experiments to find out why, and discovered that established flocks were tranquil because every hen in them “knew her place.” A so-called “peck order” had been established early in disputes over food; the winner in each battle became permanently dominant over the loser. It turns out that bird flocks often have peck orders, or, as they are now more generally called, “dominance hierarchies.”

Dominance hierarchies are not



Courtship feeding—a male Caspian Tern presents a fish to his mate.

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restricted to birds. My wife, Anne, and I have studied them in coral reef fishes by the simple expedient of carrying unbreakable mirrors with us underwater. Rarely is fighting observed in fish schools, but if a mirror is placed in the coral, members of schooling species frequently attack it viciously. They presumably interpret their reflected image as a new fish in the school, and immediately engage in combat to determine whether they should be dominant or submissive to the newcomer. We could not help but be amused by the apparent puzzlement of the fishes when they moved in front of the mirror pecking

vigorously at their image until they passed an edge and the new adversary instantly disappeared!

Once position in a dominance hierarchy is established, disputes are mostly settled by display, not combat. Normally the dominant individual will put on an aggressive display and immediately be appeased by retreat or a submissive gesture from the individual lower in the hierarchy. Thus order is kept in the group with little or no threat of bloodshed.

In birds, dominance is sometimes signalled by arbitrary symbols called “badges,” equivalent to the badge of a policeman, rather than by body size or other attributes directly related to fighting ability (such as horns in sheep). There is evidence that in Harris’ Sparrows, darkness of the head and “bib” (throat and upper breast) is a signal of dominance. When the bib is artificially dyed darker, a bird’s position in the hierarchy tends to rise, perhaps because older birds naturally have darker bibs and are better fighters. Similarly, an ingenious experiment has connected the width of a dark bib and dark stripe down the breast and belly with dominance in Great Tits, Eurasian relatives of our chickadees. Two Norwegian scientists put radio-controlled motors inside stuffed Great

Tits which they placed on feeders. When a Great Tit approached, the stuffed birds could be turned to face it and made to give an aggressive display by raising its head. Whenever the dark area was larger on the stuffed bird than on the incoming one, the intruder was frightened off.

Perhaps the most interesting bird badges yet studied occur on a common species that can easily be seen breeding by almost any North American birder—the Red-winged Blackbird. The badges of the red-wings are, of course, its epaulettes. These badges differ from those of Harris' Sparrows or Great Tits, in that they can be partly or entirely hidden. They can also be brilliantly displayed by males doing "songspreads" on their territories—arching forward, bending their spread tails downward, and spreading their wings to the side to display the epaulettes forward. The badges are often at least partially covered, however, when males are moving around and feeding.

The importance to territorial males of displaying their epaulettes was demonstrated by experiments in which the patch of red feathers of some birds were dyed black. More than sixty percent of males so altered were evicted from their territories, as opposed to fewer than ten percent of undyed males. Could this be because male red-wings seeking a territory simply did not recognize the dyed birds as members of their species? Did newcomers continue to invade the epauletteless birds' territories until the latter gave up in exhaustion? It appears not—although the dyed birds could no longer give a proper songspread display, they *were* recognizable as red-wings.

This conclusion was verified by placing stuffed male red-wing skins (red-wing "mounts"), in the field, where they could be seen by wild males. It is a technique I used almost three decades ago in an experiment to map meadowlark territories. I still

recall vividly the vigor with which territorial males attacked the meadowlark mounts. By moving the stuffed birds around and seeing which males attacked them, it was easy to map the territorial boundaries.

In the experiments testing whether male red-wings could identify individuals with blackened epaulettes, mounts with their epaulettes dyed black and mounts of male Brewer's Blackbirds, which resemble the dyed red-wings, were used. Territorial male red-wings reacted to the dyed red-wing mounts, but not to the Brewer's mounts. They could clearly recognize that the red-wings were their own species, even without epaulettes.

red-wings either seeking territories or trying to feed within the territories of other males tend to conceal their epaulettes—it greatly reduces the chances of being vigorously attacked. If a male takes up residence in a newly empty territory, he will expose his epaulettes gradually, and act like a full-fledged territory owner after about one-half hour.

Many questions remain about how displays evolve and about the relative advantages to individuals in different positions in dominance hierarchies. For instance, does being high in a dominance hierarchy increase an individual's reproductive output? Or does the energetic cost of, say, holding a prime territory on a lek



Male prairie-chicken on lek, displaying to female.

Nonetheless, epaulettes *are* a key component of male red-wing displays. Four kinds of mounts were shown to territorial male red-wings: normal ones, ones with the epaulettes half-blackened, and ones with the epaulettes doubled in size by adding feathers taken from other red-wing mounts. The strength of attacks by the territorial males was proportional to the amount of red visible. The violence of the attacks on mounts with doubled epaulettes caused considerable damage to the stuffed red-wing skins.

This result makes clear why male

reduce a dominant prairie-chicken's lifetime reproduction to about the same level as a low-ranked male who uses much less time and energy in defense and much more chasing females? The answer to this and similar questions is far from clear. What is clear, though, is that displays and dominance relationships are two key aspects of bird biology that are fascinating to observe when birding for fun.

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