Introduction
The behavior involved in courtship and pair formation has a special fascination for ornithologists because of the remarkable sounds, postures, and body actions performed by courting birds. Waterfowl have rich repertoires of these courtship "displays," and several of the most spectacular actions have become textbook examples of highly stereotyped social signals. The topic of how waterfowl communicate with one another in situations other than courtship (e.g., territory defense, brood rearing) raises broader issues related to the overall "signal system" characteristic of each species. As well as the important seasonal needs for signaling associated with these reproductive activities, there are also day-to-day requirements for signals, such as those that synchronize taking flight in pairs or family groups and those that enable individuals to compete for resources. Therefore, although signals are vitally important in courtship and pairing, this is only one aspect of the communicative behavior of each species.

Current understanding of courtship, pairing, and signaling in waterfowl can be traced back to the writings of Heinroth (1910, 1911). These classic papers were published in German, but the 1911 paper is now available in English translation (Burhardt 1985). Heinroth's perceptive observations, made primarily on captive waterfowl in the Berlin Zoo, inspired Konrad Lorenz's (1941) comparative study on the display repertoires of ducks, which played a central role in establishing Lorenz's school of ethology. The interests and perspectives of observers and researchers have changed greatly over the years, however, and many concepts and interpretations that were formerly influential are now out of fashion. In reviewing these changes I hope to draw attention to problems addressed in earlier waterfowl studies that need to be reexamined in the light of current ideas.

A revolution in thinking about social behavior took place during the 1970s. With the emergence of the disciplines of sociobiology and behavioral ecology, exciting new interpretations of courtship and signaling were developed. Researchers focused attention on the consequences of natural selection operating at the individual level (Williams 1966) and on potential conflicts of interest between males and females (Trivers 1972). Studies of social behavior became integrated into ecological and evolutionary research on social systems and reproductive strategies (see chapters 3, 6, and 8 of this volume).

As a result, emphasis on the study of adaptations directed attention to problems of the ultimate functions of behavior, while research on the development, immediate causation, and evolutionary history of social behavior—so characteristic of ethology in the 1960s—declined. At the same time, it became unfashionable to do descriptive comparative research of the classical ethological kind, and few researchers tackled analytical studies of the proximate, dynamic aspects of signaling.

I begin with a historical review of various perspectives on "displays" to illustrate how diverse the approaches have been and how influential many of them were in their day. For example, the classic studies by Lorenz (1941) and Delacour and Mayr (1945) showed how waterfowl displays can be used as taxonomic characters. This approach was greatly refined by Paul Johnsgard, who provided a descriptive catalog of displays for most living anatids in his Handbook of Waterfowl Behavior (1965a). These three impressive works were widely acclaimed by ornithologists, and for a time they established the Anatidae as the best-studied family of birds from the perspective of comparative ethology. Since the 1960s, major advances in research on social behavior and communication have come through work with other bird groups (e.g., passerine birds, shorebirds, sev-
eral seabird groups), and progress in understanding waterfowl behavior has been relatively slow. In fact, up to this point, research on waterfowl displays has had little impact on the field of animal communication, and I will not attempt to integrate the waterfowl information into the broader literature. Extensive reviews of the literature on animal communication are given by Smith (1977), Sebeck (1977), Hallman (1977), Green and Marler (1979), Kroodsma and Miller (1982), and Halliday and Slater (1983b).

Recent interest in the topic of sexual selection has stimulated research on the phenomena of mate choice and pair formation, and new perspectives on courtship have come from the development of new theory. Again, I introduce the topic of social courtship with a historical review.

The third section, on the diversity of signal systems, explores how ecological and social factors have molded communication methods in particular groups and species. This approach, inspired by the comparative studies of Crook (1964) on weaver birds (Ploceidae), has been neglected in waterfowl, and I include speculative discussions here in an attempt to stimulate further research.

II. Different Approaches to the Study of Displays

Much of the literature on the social behavior of waterfowl consists of descriptive inventories of displays. The term “display” includes postures, movements, and vocalizations that appear to function as social signals. The evidence for signal function is usually indirect; it is inferred from the stereotyped form of the movements or calls, the situations in which they are performed, their orientation with respect to other birds, and the responses they appear to elicit. Most waterfowl displays are conspicuous, discrete behavioral units with distinctive form, and most are performed as the birds swim on open water, where they are easy to observe. This means that they can be named, described, and measured accurately from film or tape. Each species has a repertoire of about 15-25 easily distinguished displays, and there are specific (often racial) differences between the repertoires. With all these convenient and intriguing features, it is not surprising that the displays of waterfowl have attracted the attention of many researchers. The interests of these researchers have varied greatly, however, and their approaches have been influenced by their diverse backgrounds. Different approaches to animal communication have been reviewed in more detail by Smith (1977) and Beer (1982).

A. Fixed Action Patterns

Courtship displays of ducks played a major role in developing the ideas of pioneer ethologist Konrad Lorenz on how the behavior of animals is organized and controlled. In particular, it was his familiarity with such displays as the grunt-whistle of the Mallard that shaped Lorenz’s (e.g., 1950) concept of “fixed action patterns” (FAPs), which he regarded as the natural units of behavior.

Lorenz believed that FAPs have a number of distinctive properties. (1) They are highly stereotyped in form, and in this sense they are reflexlike. (2) Unlike reflexes, FAPs show spontaneity: each is produced by spontaneous activity in a specific internal mechanism in the central nervous system, and each is triggered by highly specific external stimuli (“releasers”). (3) Variations in the readiness of animals to respond to releasing stimuli can be explained in terms of the accumulation (as though in a reservoir) of “energy” specific to each FAP; if the energy is denied “discharge,” the threshold for release of the FAP is lowered and the behavior is “released” with a minimum of external stimulation (or even in the absence of external stimulation—a “vacuum activity”). (4) FAPs are innate in the sense that they are performed by the animal without the need for practice or experience; i.e., they are genetically programmed.

Therefore, in Lorenz’s sense, FAPs are not merely stereotyped behavior patterns. The label implies fixity, rigid CNS control, spontaneity, and genetic determination, and on all of these points Lorenz’s views have been challenged. So widespread have these criticisms been that many ethologists no longer find the FAP concept useful (e.g., Barlow 1977; Dawkins 1983). A few examples illustrate the problems.

(1) Stereotypy. Surprisingly, the “fixity” or stereotypy of waterfowl displays has received little systematic attention. This feature has generally been taken for granted. Researchers have tended to follow Lorenz’s belief that displays are so invariant in form that they can be treated like bones and muscles, as though they are “organs possessed by the species.” Exceptions were the studies by Dane et al. (1959) and Dane and van der Kloot (1964) on the displays of the Common Goldeneye. Based on analyses of movie films, these studies revealed striking stereotypy in the durations of several displays. Most of the displays are brief actions, however, and the amount of variability between performances varies among displays. Barlow (1977) has questioned whether stereotypy in duration is really peculiar to displays, and it is true that some actions used in locomotion, body care, and feeding (e.g., pecking rates of grazing geese, Owen 1980: 133) vary little in duration.

Many displays that involve series of call notes show both intra- and interindividual variation (e.g., number of notes in the decrescendo calls of Anas females, Abraham 1974). Other displays are variable in form and may grade into one another (e.g., threat postures of geese, Fischer 1965). Few attempts have been made to analyze
spatial aspects of display performances (e.g., McKinney 1975; Pellis 1982; Finley et al. 1983) and little is known about variation in these parameters. In short, although many waterfowl displays have a stereotypic form, many are quite variable.

(2) Spontaneity. There is abundant evidence that environmental factors of various kinds can influence the occurrence of specific displays in particular situations, their presence in display chains, and their orientation in respect to other birds (e.g., Simons and Weidmann 1973). A releaser-like triggering phenomenon may be involved in certain cases (e.g., in some circumstances a nod-swimming female Mallard may stimulate a burst of male displays) and some display chains do tend to be highly stereotyped (e.g., grunt-whistle + head-up-tail-up + turn-toward-female in many Anas species), but the neurophysiological mechanisms mediating these performances are unknown and likely to be much more complex than Lorenz envisioned. Attempts to demonstrate control of complex display performances by electrical stimulation of central nervous system structures have not been successful in Mallards (Phillips and Youngren 1973), and this technique no longer seems promising as a tool for studying communication (R. E. Phillips, pers. comm.) While recent research on invertebrates provides support for Lorenz’s CNS control view of FAPs (see Dawkins 1983), similar mechanisms cannot be assumed to operate in birds.

(3) Action-specific energy. There has been much criticism of the Lorenzian energy model of motivation (e.g., Hinde 1970), and it is now generally recognized that many mechanisms can be involved in the causation of behavior. In situations where the threshold appears to be lowered for the performance of a particular type of behavior, it is necessary to explore various kinds of causal mechanisms rather than assuming the “damming up” of “action-specific energy.” Alternative motivational models are being actively explored.

(4) Genetic control. The genetically programmed aspect of fixed action patterns remains a little-studied topic in waterfowl. Breeding experiments involving the production of interspecific hybrids have provided evidence on the genetic control of certain duck displays (Sharpe and Johnsgard 1966). On the other hand, studies of the development of bird displays indicate that learning and/or maturational processes are involved (Kruit 1964; Groothuis, 1989). Early performances of displays by young ducks are often incomplete and inappropriately oriented; some displays of adults are absent from the juvenile repertoire; and some displays performed by juveniles do not occur in the adult repertoire (Dane and van der Kloot 1964; Kaltenhauser 1971; Korschgen and Fredrickson 1976).

In summary, while many waterfowl displays are highly stereotyped, this does not mean that they have all the characteristics that Lorenz attributed to FAPs. Most ethologists now avoid the term because it carries with it these Lorenzian implications. Neutral terms such as “action pattern” or “behavior pattern” (e.g., Drummond 1981) are often used instead. Historically the FAP concept was important because it helped to focus attention on displays and probably stimulated research on them.

B. Motivational Conflicts

The mechanisms whereby external stimuli and internal states of the animal interact to produce behavior should be explainable in terms of neural and hormonal processes. Nevertheless, many ethologists have argued that “software” explanations are also needed. As Hinde (1982: 3) explains, “They specify the relations between stimulus and response, between antecedent conditions and motivational states, between motivational states and behaviour, and between different sorts of behaviour, without specifying the hardware—the neural and other mechanisms on which those relations depend.”

Motivational concepts such as “thirst,” “hunger,” “aggressive drive,” and “sexual tendency” have been used widely in describing and classifying observed behavior, but the value of such “intervening variables” has been debated for many years. They are avoided by many workers who feel that careless use of the concepts can lead to circular reasoning; others continue to use them, but cautiously, often as convenient “labels for unknown physiological processes” (Halliday 1983). Much current research on motivation is based on sophisticated laboratory experiments and models derived from control theory, but from the 1940s to the 1960s the ethological literature on the causation of behavior was dominated by controversies sparked by conceptual models that have now been discarded or greatly modified (see McFarland 1971; McFarland and Sibly 1975; Toates and Halliday 1980; Halliday and Slater 1983a; Huntingford 1984; Colgan 1989). As a result, caution and skepticism are required in evaluating writings on waterfowl behavior from this era.

A reexamination of Lorenz’s classic 1941 paper (most recently translated into English by Robert Martin [Lorenz 1971]), shows how strongly Lorenz’s view of duck courtship was influenced by his ideas on internal motivating factors. For example, he suggested that the introductory shakes given by male Mallards at the beginning of a bout of social courtship may “serve for self-stimulation of the drake.” He thought that the birds need to “work themselves up” in a motivational sense before they are able to perform any of the “real” courtship displays. Later research, focusing on environmental cues, has suggested the alternative explanation that shakes notify the female of the male’s interest in her, enabling males to time the performance of their subse-
quent displays for maximum effect in attracting female attention and competing with rivals.

There are many other ways in which thinking in terms of the bird's supposed motivational state influenced early views on waterfowl courtship. The discovery of "displacement activities" in the 1940s was especially influential. As interpreted by Tinbergen (1952), these are out-of-context, apparently irrelevant actions that animals perform in moments of motivational conflict or thwarting. Familiar examples are pecking at the ground by cockerels during fighting, grass pulling by gulls during territorial encounters, and the preening movements of ducks during courtship. Inherent in the original concept was the idea that "there is a surplus of motivation, the discharge of which through the normal paths is in some way prevented" (Tinbergen 1951: 114). Later, when Lorenz's energy model of motivation was rejected by many workers, alternative causal hypotheses for displacement activities were developed (reviewed by Halliday 1980; McCleery 1983). It became apparent that a single causal mechanism was not involved in all cases, and analytical studies of specific displacement activities showed that they were not really "irrelevant" (i.e., nonfunctional) as had been supposed. Therefore, as with the FAP concept, the term "displacement activity" has become outmoded and of little use as a label for a particular category of behavior patterns. The problem of how to deal with this concept is not trivial, because most authors of textbooks on animal behavior continue to refer to displacement activities in discussing the evolutionary origins of displays and rarely include a review of how ideas in this field have changed.

Historically, displacement activities were important because they stimulated Tinbergen's (1952) thinking about the role of motivational conflict in the evolutionary origins of courtship and threat displays. As Baerends (1975: 203) pointed out, however, this conflict hypothesis "was developed for explaining how some display activities obtained their form in the course of evolution and although it has often been extended for explaining causation, such attempts are likely to become less rewarding with increasing emancipation of the displays." ("Emancipation" [Tinbergen 1952] refers to the changes in physiological mechanisms that are expected to accompany the evolution of a display from a nonrationalized precursory action). The seriousness of these difficulties was not appreciated in the excitement over the idea that displays can be interpreted as "compromises" between opposing, incompatible tendencies (e.g., to attack vs. to flee). For example, Tinbergen and van Iersel (1948) argued that the stickleback's zigzag courtship "dance" can be understood as a ritualized action derived from rapidly alternating intention movements of attacking the female and leading her to the nest. Similar kinds of interpretations have been helpful in suggesting evolutionary origins for inciting in female ducks (Lorenz 1941), the triumph ceremonies of geese (Lorenz 1965; Fischer 1965; Raveling 1970; Radesater 1975a), and the preflight activities of geese (Raveling 1969). In these cases, the displays appear to have retained strong elements of the conflicting motivations underlying the social situations concerned; i.e., they have not become fully "emancipated" from their original motivational bases.

Early attempts to use this approach to analyze the threat displays of gulls (Moynihan 1955, 1962), geese (Blurton Jones 1960), and courtship in general in terms of conflicts between mating, attack, and escape tendencies (Morris 1956) stimulated similar interpretations of duck displays (Moynihan 1958; Lind 1959; McKinney 1961). These duck studies showed that each display occurs in one or more well-defined social situation, and that many of these situations involve hostility (the presence of attack and escape "tendencies"). They also led to some suggestions on evolutionary origins and signal functions of the displays. Many researchers considered the motivational approach more distracting than helpful, however, primarily for the reason noted by Baerends. Thus Dane and van der Kloot (1964: 323) concluded: "The attempt to assign a specific drive to each of the display actions and then to account for display in terms of the waxing and waning of these drives may be more confusing than illuminating." Nevertheless, the approach is still being used, with more sophisticated developmental, experimental, and modeling methods, to analyses of gull displays (Veen 1987; Groothuis 1989).

In summary, a focus on the motivational state of the signaler was characteristic of much early research on waterfowl displays. Although helpful in suggesting probable evolutionary origins for certain displays, this approach has encountered serious difficulties. Many duck displays are probably largely emancipated from the motivational context in which they evolved and attempts to assign each display a specific conflict pattern entails highly speculative deductions about the bird's motivational state. It should be noted that the ideas of "conflict" and "compromise" are currently proving to be extremely valuable in studying behavioral adaptations. Here the focus is on conflicting selection pressures (e.g., those promoting mate guarding vs. extrapair copulations), the trade-offs in terms of individual lifetime reproductive success, and proximate questions relating to how animals actually make choices between competing activities.

C. Evolutionary Origins of Displays

As well as being concerned with motivational issues, many early ethological studies led to ideas on the origi-
nal sources of display movements and the processes involved in signal evolution. The most easily identified sources are comfort movements (such as preening, bathing, and shaking), feeding movements, and locomotory actions (e.g., Lorenz 1941; Johnsgard 1962, 1965; McKinney 1965a, 1970). In many cases, displays derived from these movements differ only slightly from them in form (e.g., exaggeration of certain components, rhythmical repetition), and they provide excellent examples of the evolutionary process of ritualization. Characteristic positioning and body orientation of the performer in relation to the target bird is usually an integral part of such displays, and special body structures and plumage patterns may be shown off during the performance. In the duck tribes, these kinds of easily derived signals (e.g., freen-behind-wing) are especially characteristic of situations in which paired birds exchange precopulatory or bond-maintenance signals.

One important consequence of this early interest in display origins was that many previously unrecognized displays were discovered. Careful analyses of particular species on film often showed that different displays had previously been confused with one another, subtle displays had been overlooked, and some displays were rare rather than absent from the repertoire. As a result, the waterfowl literature is very uneven with respect to the comprehensiveness of catalogs of display repertoires. Detailed, fine-grained ethograms are available for some species. Superficial accounts for many others. There is no up-to-date review of information on display repertoires available. Interest in compiling detailed descriptions of display repertoires has declined, and it is now difficult to publish such studies.

D. Displays as Taxonomic Characters

Although Heinroth (1911) recognized the possibility, it was Lorenz (1941, 1971) who pioneered the deliberate search for homologous displays and their use as indicators of taxonomic relationships within the Anatidae. Lorenz plotted the distribution of 33 behavioral characters in 18 species (13 dabbling ducks, 3 perching ducks, 2 shelducks) and arranged them (along with various morphological characteristics) in his famous "shaving-brush" diagram. In this way he showed, for example, that each of these groups has distinctive precopulatory displays (head-pumping, aiming, and neck-dipping, respectively), and that the presence of neck-dipping in shelducks indicates their close relationship to swans and geese, which have very similar (presumably homologous) displays.

One of Lorenz's main objectives was to arrange the dabbling ducks in natural groups by using the presence or absence of certain diagnostic displays in each species. For example, he grouped the Gadwall with two wigeon species (linked by the presence of chin-lifting), and separated our two green-winged teal species (sharing the "koedick" call), from three pintail species (with distinctive postures and calls in female inciting), and two blue-winged ducks (linked by the presence of head-pumping during inciting). By examining the distribution of the "major" Anas courtship displays—grunt-whistle, head-up-tail-up, bridling, and down-up—Lorenz concluded that the wigeons and the blue-winged ducks (which lack these displays) should be placed as side branches on his diagram. Thus he viewed his diagram as a phylogenetic tree.

Lorenz deliberately applied the methods of comparative anatomy to behavior, and he was well aware of the difficulties of identifying homologous displays. Homology implies that the same display was present in the common ancestor of the species being compared, just as anatomists imply the presence of a trait in a common ancestor when they homologize the humerus of a bird and a mammal. The problem is to distinguish truly homologous displays from similar but nonhomologous displays evolved independently. Lorenz discussed this problem in comparing the grunt-whistle of Anas species with the similar courtship displays of Aix. After examining the form of the movements in the two groups, Lorenz concluded that the displays were not homologous but had evolved independently from body-shaking movements. Of course such judgments can be contested and there are many possibilities for controversy over attempts to identify homologous displays within the Anatidae.

In spite of the difficulties and uncertainties of the method, Johnsgard (1961a, 1965, 1978) followed Lorenz's lead and made extensive use of behavioral characters in his revisions of anatid taxonomy. For example, displays were very important in indicating that the affinities of the White-backed Duck are with the whistling ducks (Dendrocygnini) rather than the stifftails (Oxyurini), to which this species had formerly been assigned (Johnsgard 1967).

The strongest test for the use of behavioral characters in taxonomy is to compare findings based on behavior with those reached using different techniques. Fortunately, there have been many independent analyses of anatid taxonomy, and recent results using immunoelectrophoresis (Botter 1983), DNA-DNA hybridization (C. G. Sibley et al. 1988; Madsen et al. 1988), and morphological characters (Livezey 1986, 1991) have supported most of Johnsgard's taxonomic alignments.

There remain several intriguing species whose relationships within the family are uncertain. For example, the affinities of two river specialists, the South American Torrent Duck and New Zealand's Blue Duck, have long been disputed. Because anatomical similarities between them might reflect common ancestry or convergent ad-
aptations for river dwelling, behavioral evidence is of special interest. The latest attempts to detect homologies between the displays of these two species and those of other anatids were unsuccessful and led Eldridge (1979, 1985) to conclude that both species have long been isolated from other waterfowl groups. This negative evidence is consistent with the sedentary lifestyle of these species and their widely separated geographic ranges.

In summary, comparative studies of display repertoires can reveal useful taxonomic characters, and the method has been well tested in the waterfowl. While there is already a rich literature on the display repertoires of anatids, more detailed and refined analyses of certain tribes could be profitable in the future, especially if they are prompted by new hypotheses on the phylogenetic history of the family (Burghardt and Gittleman 1990). Recent comparative analyses of bird songs (Payne 1986) suggest that waterfowl vocalizations deserve more attention than they have received to date (e.g., Kear 1968).

E. Displays as Isolating Mechanisms

The search for displays that could be used as taxonomic characters revealed distinctive features of the display repertoires of each waterfowl tribe. Some of these characteristics can be related to morphology and lifestyle (e.g., variations in body size and proportions, locomotor abilities, and feeding methods); others may have their roots in the evolutionary history of each tribal stock, and so may be difficult to trace. At the same time, specific and racial variations in display repertoires have been discovered. Indeed, every new study of the repertoire of a previously undescribed species or race can be expected to reveal unique features distinct from the repertoires of even the closest relatives. The factors responsible for these changes in signal repertoires during the course of anatid evolution pose intriguing problems.

During the 1950s and 1960s there was much interest among evolutionary biologists in “isolating mechanisms” that allow species to maintain their genetic integrity. These were defined by Mayr (1963) as “biological properties of individuals that prevent the interbreeding of populations that are actually or potentially sympatric.” In birds such as dabbling ducks, females were thought to choose males of their own species as mates instinctively, the choice mechanism apparently depending on species-specific Lorenzian “releasers” in the form of male plumage and courtship patterns. Sibley (1957) proposed that “it is these signal characters, or isolating mechanisms, which are enhanced by the reinforcement which occurs when interspecific hybrids are selected against.”

This line of reasoning was followed by Johnsgard (1960b, c, 1962, 1963) in reviews of the evidence on hybridization and potential isolating mechanisms in Anatidae. He showed that instances of hybridization have been recorded in many tribes within the family, both in captives and in wild populations of sympatric species, and because hybrids between closely related species are often fertile, he argued that behavioral isolating mechanisms must be operating effectively to maintain species integrity. On the basis of a review of morphological and behavioral differences among sympatric species, Johnsgard (1963) concluded that, in general within the family, “vocalizations and male plumages and soft-part features are probably of greatest importance in preventing hybridization between closely related species, and male courtship displays are only slightly less important in this regard.”

In support of the argument that diversity of male display repertoires in ducks can be attributed largely to selection for efficient isolating mechanisms, Johnsgard (1965, 1968) showed that divergence tends to be more marked in those displays that are important in pair formation than in those associated with pair-bond maintenance and copulation. This would be predicted because selection should favor correct species identification as early as possible in the reproductive cycle, so as to avoid wastage of time, energy, and gametes. Second, Johnsgard (1960c) showed that, in general, male courtship display repertoires (and male plumage patterns) are more diverse in the subfamily Anatinae than they are in the Anserinae, and sexual dimorphism in plumage is more prevalent in the former tribes. Johnsgard linked these differences to the major differences in pair-bonding characteristic of each subfamily. He argued that effective species-recognition signals may be much more important in the Anatinae than in the Anserini, because ducks typically form new pair-bonds each year and there is much greater sympathy of closely related species among ducks.

One way to test this hypothesis was to look for indications of relaxation of selection for distinct species-recognition signals in regions where the risks of hybridization are greatly reduced. Sibley (1957) sought evidence of this kind among Anas species in different parts of the world, contrasting them with holarctic regions, where most sympatric dabbling duck species have diverse male plumages and specific differences in pairing seasons. He noted that certain island forms (with few or no sympatric congeners) have lost their bright male plumages. Some sympatric South American species have reduced plumage dichromatism (perhaps associated with long-term pair-bonding) but they do have distinctively different male displays and bill patterns that could serve as isolating mechanisms. Although most sympatric African species show reduced sexual dichromatism, Sibley suggested that they may be more ecologically isolated from one another than are holarctic forms. Many
suggestions along similar lines were offered by Johnsgard (1965, 1968).

Subsequent research has shown that many of the broad comparative generalizations on which this hypothesis was based are weakened by exceptions and that alternative sources of selection could have shaped the evolution of courtship display repertoires (West-Eberhard 1983; Payne 1983). Assumptions about behavioral mechanisms need to be revised in the light of these new findings. It may prove difficult to demonstrate conclusively that selection against hybrids has been a factor in the evolution of elaborate and specifically distinct courtship display repertoires. One possibility is to examine divergence in behavioral repertoires within individual species in areas of sympatry and allopatry (character displacement). So far, however, in studies of passerine bird songs this approach has not been encouraging, in spite of a seemingly rich source of possibilities among vocalizations known to be important in species-recognition (Becker 1982).

Major difficulties with the displays-as-isolating-mechanisms hypothesis are the assumptions that were made about the mechanism of pair formation and the factors influencing mate choice in dabbling ducks. Sibley (1957: 179) argued that females must “instinctively” choose a male of their own species because males leave their mates before the eggs. As a result females have no opportunity to learn to recognize males “through early contact with their own male parent.” He dismissed “the possibility that ‘imprinting’, or any other primitive learning process” is involved. Subsequent research has shown that influences of early experience during the brood phase are very important in shaping preferences of birds for mates of a type similar to the parent and siblings with which they grew up (see section III.D).

Although the displays used by male ducks in courtship are more diverse among species than either precopulatory displays or the displays of females, this does not necessarily mean that distinctive male repertoires are essential to ensure that females choose mates of the correct species. Detailed knowledge is needed of the processes involved in courtship and mate choice in individual species. The evidence available for several species indicates that (a) male displays are very likely shaped primarily by sexual selection, (b) they appear to serve a variety of signal functions during social interactions, and (c) dominance relationships between males may be as important as female choice in determining whether hybrid matings occur (section III).

While it is true that males of many island races of ducks are less brightly colored than the mainland counterparts from which they are presumed to be derived (Weller 1980), these plumage changes need not have been related to reduced needs for species distinctiveness. Alternative possibilities are that they are related to pre-
easily), and there is no reason to suppose that complex multicolored plumages are "necessary" to enable birds to recognize specifics. It has not yet been demonstrated that the sounds and movements involved in the courtship displays of ducks are crucial for species recognition. Experimental studies designed to reveal the cues that are involved in this fundamentally important process are badly needed.

F. Displays as Social Signals

Students of waterfowl behavior usually have few problems distinguishing movements, postures, and vocalizations that serve as social signals (i.e., displays) from nonsignal behavior. It is much more difficult, however, to determine what information is being transmitted and what effects the signals have on the birds that receive them. Experimental approaches using playback of taped vocalizations have been used to investigate communication between ducklings and their mothers (Gottlieb 1971; Miller 1980), and between ducklings (Gagnon 1982; Gagnon and Evans 1985), goslings (Lampecht 1983), and mates (Lockner and Phillips 1969; Abraham 1974), but experimental methods have not been devised for visual signals.

Indirect evidence on signal functions can come from analysis of the social interactions in which the signals are given. Four kinds of evidence help both to identify a signal and to provide clues to its function(s): (a) the situations in which the display is performed (e.g., other birds present, temporal relationships to other activities); (b) the characteristics of the display (duration, temporal patterning, morphological features shown off); (c) the spatial orientation of the display (which can indicate the intended receiver of the message); and (d) apparent effects or consequences of the display (changes in the behavior of the receiver). I will illustrate each of these sources of information with a few examples.

1. Display Situations

Good examples of displays whose function can be inferred with confidence because of contextual information are preflight signals, which are conspicuous in all waterfowl tribes. They entail facing into the wind and assuming an erect posture with head held high (often with synchronized swimming and turning by the birds in a group), ritualized movements (usually up and down) of head and/or neck, a variety of comfort movements (e.g., body-shakes, wing-flaps, wing-and-leg-stretches), and, in some species, loud calls. These are classic examples of Heinroth's (1911) "intention movements," and they are diagnostic of birds that intend to take wing. Although preflight displays are sometimes given by isolated birds, their use as signals is obvious when they occur in a pair, family group, or flock. At first, one bird begins to perform; if others do not join in, the initiator usually does not fly. If the initiator's "suggestion" is agreed to, others join in, the pace quickens, and eventually they take off simultaneously. We infer that these signals function in promoting synchronous takeoff by the members of the group.

The importance of preflight signaling in coordinating takeoffs is especially striking in pairs and families of geese and swans (Raveling 1969; Black and Barrow 1985; Black 1988). Raveling (1969) studied this behavior in Canada Geese, including individually marked families. The most obvious preflight signal of this species is head-tossing, in which the bill is pointed upward and shaken from side to side with a tossing motion. Raveling found that any member of the family can begin preflight behavior, but the gander is the crucial bird in deciding when the family will take off. When the gander initiates head-tossing, the other family members join in quickly and takeoff occurs soon thereafter. If another family member is the initiator, takeoff is delayed until after the male joins in. Vocalizations and plumage patterns appear to be important also in promoting simultaneous takeoff in geese. In Canada Geese, low guttural calls are given during the preflight activities, then just before takeoff these change to a crescendo of loud honking, and the white rump patch is exposed as the wings are lifted out of their "pockets."

Ritualized preflight movements are generally similar within each genus or tribe (Johnsgard 1965; McKinney 1965a), but the calls given in this situation and the plumage patterns exhibited (e.g., the specula of ducks, and the conspicuous, contrasting markings on the back and tail of geese) are usually distinctively different in each species (Heinroth 1911; Raveling 1969; Owen 1980). In ducks, preflight behavior commonly involves pair members and, in contrast to the situation in geese, the female usually seems to determine when the pair will fly (Hochbaum 1944; Sowls 1955; Derrickson 1986). Dabbling ducks such as the Mallard give quiet vocalizations before takeoff, then a series of loud contact calls as the pair flies up. When takeoff is delayed for some time, distinctive ritualized head-shake and chin-lifting displays are given, and a variety of nonritualized comfort movements may also be performed (wing-flaps, wing-stretches, preening, bathing) (McKinney 1965a).

2. Display Characteristics

Detailed study of postures and movements of body parts can also provide clues to the signal functions of displays. For example, during hostile encounters many species adopt postures with head lowered and bill pointed toward the adversary. These displays are also examples of "intention movements" in that they appear to have evolved by ritualization of the body posture involved in an actual attack. Examples are the head-low and forward posture of Dendrocygna, forward of Anser and
Branta, head-forward of Bucephala, and hunched rush of Oxyura (see figures in Johnsgard 1963). All of these displays have been interpreted as functioning as “threat signals”; i.e., they tend to produce the withdrawal of the opponent. In these cases, of course, the orientation of the bird in relation to its opponent, the situation (the posture may be followed by a real attack), and the effect (the opponent often withdraws) are also used to support the threat-function interpretation.

One method that has been used to deduce signal function of more complex displays is to look for the presence of postures or movements that resemble intention movements of attack, such as the head-low, bill-pointing postures discussed above. The assumption is that, no matter what the situation, these postures will convey a threat signal to the target individual. This idea has been discussed in detail by Morton (1977, 1982) in regard to the motivational-structural rules that appear to apply to some avian vocalizations. In waterfowl, the application of this idea is especially well illustrated by the so-called inciting displays of female ducks.

The term inciting is widely used in the literature to refer to displays of paired or courted females that simultaneously indicate affiliation with one male and rejection of a rival courting male. In many ducks (e.g., Tadorna and Aythya species) inciting involves two different head movements performed alternately: the female lowers her head and points her bill directly at the rejected bird and then raises her head high as she turns back toward her mate. The aggressive nature of the pointing movement is obvious because at times the female follows the posture with an aggressive rush. The exact form of the head movements directed at the mate varies among species, as do the accompanying calls, but the overall pattern of the performance and the circumstances in which it is given are similar across a wide range of tribes. As the English word inciting implies, and as Heinroth (1911) described in shelducks, this behavior appears to stimulate the female’s mate to attack the rival in certain species. The term is really inappropriate in many species (e.g., dabbling ducks), because the mate rarely responds (at least not immediately) by showing overt aggression; nevertheless inciting is still used as a label for the display. In the latter species, the display apparently sends two messages: a “friendly” demonstration of preference, acceptance, or allegiance to one male, and an “unfriendly” show of rejection toward another.

In dabbling ducks such as the Mallard and Northern Pintail, inciting has become highly ritualized and it is less easy to detect the two components from which it is believed to have evolved (Lorenz 1958). The head movements are reduced to short, repeated, sideways jabs “over-the-shoulder” and they are accompanied by a distinctive, loud, rhythmic call. An analysis of the orientation of the female Mallard’s body and head has shown, however, that at some point during the performance her bill still points directly at the rejected male (Stillwell and Hailman 1978).

Inciting has also been recorded in other situations: by a female Mallard to her mate in the absence of any other bird (Weidmann 1956), by a female Blue-winged Teal alone with her brood while threatening other ducks that approach (McKinney 1970), by a female Speckled Teal beside her mate threatening a rival female (unpublished observations), and by a female Canvasback associating with other females when rejecting approach by a courting male in midwinter (M. G. Anderson, pers. comm.). Therefore, although the display is most familiar in the female + mate + rival male situation, it is also used in various other circumstances involving attachment and/or threat.

3. Display Orientations

The importance of studying the orientation of displays is worth emphasizing because this approach deserves more attention than it has received to date. Although the literature on the courtship displays of ducks is extensive, there have been few detailed analyses of the body orientations of the birds as they perform the displays. A start has been made in studies of Northern Pintail, Green-winged Teal, and North American Wood Duck (Smith 1968; McKinney 1975; Korschgen and Fredrickson 1976), and further analyses of this kind are included in several unpublished theses (Field 1970; Standen 1976; Schommer 1977; Wishart 1983a). Most Anas courtship displays involve broadside orientation of the male’s body in relation to the female, but others entail facing directly toward her or maneuvering to show the back of the head to her (Fig. 7-1). Even more subtle indications of the target bird can be detected by detailed film analyses of the right-left asymmetries in ritualized shaking movements, as demonstrated by Simmons and Weidmann (1973) for swimming-shake, head-flick, and headshake displays of the Mallard.

Displays such as the grunt-whistle of dabbling ducks provide some of the most striking avian examples of very precisely directional signals. This can be appreciated best by viewing a slow-motion film of a courting party of males as they swim around a single female repeatedly performing displays. In Green-winged Teal, for example, such courting groups frequently form in late winter and spring, and the orientation of male displays has been documented from films (McKinney 1965b, 1973). Each male prepares for a grunt-whistle by maneuvering his body into a position 1.0-1.5 m away from the female and exactly broadside to her. He then gives one or two rapid head-shakes, and, if his position remains favorable and if no rival male interrupts him, he proceeds into the grunt-whistle. He arches his body upward, dips his bill-tip into the water and flicks it side-
ways so as to direct a spray of water droplets at the female, emits a sharp whistle and a deep grunting sound, and subsides back on to the water while giving a head-flick. The whole performance lasts about 1 second. If the male’s position in relation to the female remains favorable, the male frequently proceeds directly into the head-up-tail-up (+ whistle) and turn-toward-female displays. The latter entails a 90 degree turn so that the male faces toward the female.

The precision of the orientation components in this chain of displays provides strong evidence that the intended target for the signals is the female, and that the messages being sent are visual (via sudden, striking movements, reinforced by bright plumage patterns), auditory (via grunt and whistle), and tactile (via water droplets). It is difficult to avoid the conclusion that these signals are designed to attract the female’s attention to the performing male and to notify her of his interest in her. Other male displays performed during social courtship (e.g., bill-up, nod-swim) appear to be designed primarily as signals to rival males. Bill-up is performed in a

hostile situation as a male approaches very close to a rival, and it seems to function as a threat signal. Nod-swimming often entails avoidance of an approaching male; it is nonaggressive and may inhibit aggressive behavior toward the performer. The latter conclusion was supported by an analysis of dominance relationships among the males and by examining consequences of the display (Laurie-Ahlberg and McKinney 1979).

The triumph ceremonies of swans, geese, shelducks, and various other waterfowl represent a complex signaling situation, but again the signal functions can be deduced (at least in very broad terms) by looking for the presence of aggressive components and by examining body orientations. In its simplest form, a triumph ceremony occurs when a pair of geese approach a strange goose: the male rushes aggressively at the stranger, then immediately turns around and rushes back to his mate while facing obliquely toward one another, both mates call together loudly while waving their necks. As Heinroth (1911; in Burghardt, 1985, p. 261) described it in Anser: “The animals look as if they would attack each
other at any moment. They usually scream their loud calls directly into each other's ears while holding their necks greatly outstretched with their heads only a bit above the ground. Even the tiny, downy young join vocally in this triumphant call and completely assume the posture of the adults.” Here the male appears to be sending similar messages as female ducks do by inciting—threat toward the stranger and affirmation of allegiance toward the mate—but this is a different kind of signaling situation because more than one bird always participates in the performance. Indeed triumph ceremonies are excellent examples of mutually cooperative “formalized interactions” (Smith 1977).

Subsequent studies of triumph ceremonies in geese have confirmed and extended Heinroth’s observations (Fischer 1965; Raveling 1970; Radesater 1974a, b, 1973a, b; Akesson and Raveling 1982; Black and Owen 1988). Triumph ceremonies occur during pairing, and pair-bonds are not fully established until the female responds actively by joining the male in the mutual posturing and calling. They occur also between mates and family members when they come together after a separation (“greeting ceremonies”), and between goslings and their parents or siblings during hostile encounters with other geese in winter flocks. Studies of the development of these ceremonies in goslings and analyses of the details of the performance in different situations clearly show that the participants are aggressively aroused. During the first 1-3 weeks of their life, the goslings within a family often threaten and fight with one another, but thereafter they more frequently use appeasing postures and orient threat postures obliquely to their siblings during family triumph ceremonies.

4. Effects of Displays
Identifying short-term effects and establishing long-term consequences of displays are among the most challenging aspects of the study of social signaling. Several examples have already been given of how signal functions of displays can be inferred by looking for immediate responses or effects (e.g., withdrawal of the target bird in response to threat displays, coordination of takeoff by means of preflight displays). Contact calls of separated mates that produce prompt replies and subsequent reunions (e.g., female decrescendo calls in Anas, Lockner and Phillips 1969) are particularly convincing, as are responses of parents to distress calls from their ducklings and the assembly of young in response to alarm calls by parents.

But many displays do not have immediate and obvious effects. The functions of postcopulatory displays are uncertain, and it is difficult to devise tests for alternative hypotheses regarding their significance (e.g., McKinney 1975). Two characteristic vocalizations of breeding dabbling ducks—persistent quacking given by females during the prelaying phase (Abraham 1974; McKinney et al. 1990) and repeated calls of “waiting males” while their females are on the nest (Dwyer 1974)—usually have no immediately discernible effects and their signal functions need to be demonstrated. In such cases, functional analysis via playback techniques, as Nuechterlein (1981) has done for the advertising display of Western Grebes (Aechmophorus occidentalis), might be fruitful.

Long-term consequences of displays have received little attention in waterfowl, but their importance is nicely illustrated by recent research on Barnacle Geese (Owen et al. 1988; Black and Owen 1988, 1989a, b; Hausberger and Black 1990). There is now evidence for this species that triumph ceremonies are (a) components in the process of mate assessment and pair formation, (b) mechanisms for reinforcing the bonds between mates, between parents and their goslings, and between siblings, and (c) collaborative threat displays used by mates and family members in competing for resources. The value of maintaining pair and family bonds, in terms of the lifetime reproductive success of individuals, has been demonstrated convincingly (also in swans by Scott 1980, 1988). Mates need to collaborate in securing and holding territories and nest sites, in caring for the goslings until they can fly, and in providing support for juveniles during migration and while the family remains together on wintering grounds. Family bonds are important for adults as well as for young, because families dominate pairs and single birds in wintering flocks, and probably also because goslings assist their parents by sharing the costs of vigilance and aggressive interactions.

It should be noted that virtually all sources of evidence on the signal functions of displays have been used in analyzing the triumph ceremonies of geese, and research on all four kinds of ethological questions—causation, development, function, and evolution (Tinbergen 1963)—has been relevant. Investigation of long-term consequences of these ceremonies calls for thorough understanding of the factors favoring long-term monogamy and extended family life. This entails integration of behavioral research with ecological information on feeding, bioenergetics, and demography. So far this level of analysis has been possible only through long-term studies on a few species of swans and geese.

G. Conflicts of Interest and Selfish Signalers
The ideas of Trivers (1972) on conflicting interests between males and females have been integrated into much recent research on mating systems (chapter 6) but they have implications also for studies of signaling. Earlier approaches to the study of waterfowl displays frequently assumed or implied that communication by displays entails mutual benefit for sender and receiver.
Displays are still widely viewed as devices whereby accurate information about the sender is transmitted to other birds. In recent years, however, increasing attention has been given to the possibility that in certain circumstances (e.g., as in interspecific distraction displays), signaling is a means whereby the sender manipulates the behavior of the receiver for the sender's benefit.

This approach was argued in stimulating discussions by Dawkins and Krebs (1978), and Krebs and Dawkins (1984). The main thrust of the argument is that we should expect signals to evolve by coevolutionary processes between the roles of "manipulator" (altering the behavior of others to the signaler’s advantage) and "mind-reader" (anticipating the behavior of others). Thus, instead of viewing the displays that males direct toward females during courtship as open transmission of information about the sender, they could be viewed as instruments of persuasion and perhaps even deception. On the other hand, cooperative signals, such as the contact calls exchanged between mates, can be expected to have different characteristics if they benefit sender and receiver equally. These ideas are being debated in the literature on animal communication (e.g., Wiley 1983; Smith 1986; Harper 1991), and they are likely to stimulate much future research.

Trivers's (1972: 150) suggestion that individuals may need to guard against "mal-treatment at the hands of one's mate" is particularly compelling in the case of mate-desertion. The consequences of being deserted by one's mate are likely to vary depending on the timing (Maynard Smith 1977). When the costs are high (in terms of lifetime reproductive success), individuals can be expected to spend most time and energy reinforcing their pair-bonds. Anderson (1984) investigated this question by measuring the relative frequency with which male and female Canvases reaffirm their pair-bonds at different stages in the breeding season. He made predictions on which sex should be most active in initiating affiliative behavior (e.g., mutual neck-stretches) at each phase based on hypothetical patterns of cumulative reproductive effort. In general, shifts in relative male and female bond-reinforcement efforts coincided with major changes in investment (and cost of desertion). The study indicated that parental investment-related desertion costs do influence this behavior but that other factors (e.g., effort expended in securing a mate, subtle assessments of mate quality) also may influence individual decisions on how to behave toward the mate.

Manipulative antidesertion tactics appear to be used by female Cape Teal and Speckled Teal in bigamous relationships (Solen and McKinney 1983; McKinney 1985). In both species, incubating females initiated copulation sequences with their bigamous mates by adopting the Prone receptive posture shortly after leaving their nests on recesses. A likely explanation for this behavior is that copulation solicitation was being used as a mate-holding tactic: the rivalries between the females were intense, and generally female ducks show no interest in copulating after they begin incubation. Preservation of the pair-bond through the incubation phase could be especially valuable for females of these species because males often accompany females with their broods and males may contribute to care of the ducklings (Siegfried 1974; McKinney and Brewer 1989).

There are also opportunities for a selfish signaling approach in studies of feeding flocks and courtship groups. For example, Black (1988) has applied the ideas of Krebs and Dawkins (1984) on "manipulators" and "mind-readers" in his studies of preflight signaling in swans. New studies are needed to elucidate the selfish tactics being used by participants in courtship groups of ducks. This will require information on the dominance status of individuals and, at least in the case of sedentary populations where individuals know one another, knowledge of the history of individual relationships may be essential as well (see section III.C).

### III. Courtship and Pair Formation

#### A. Terminology

Although much has been written about the relationships between courtship and pair formation in waterfowl, many basic questions remain unresolved. One reason for our poor understanding of these topics is that most research has been done on migratory species in which pairing occurs in large mobile flocks remote from breeding grounds. Second, even in studies of sedentary populations, few field workers have followed the behavior of individually marked birds. Therefore, most information on this topic is circumstantial and correlational, or derived from experiments on captive birds.

Some biologists (e.g., T. R. Halliday, in Harré and Lamb 1986) narrowly define "courtship" as: "behavior patterns, often very elaborate and conspicuous, that precede, accompany and sometimes follow the act of mating." Others (e.g., R. A. Hinde, in Campbell and Lack 1985) prefer a broader definition that includes "a wide range of activities of which the function seems to lie in attracting a mate, maintaining the pair bond, and in facilitating copulation and parental activities." Such broad definitions are not customary in the waterfowl literature where the activities of courtship and copulation are almost always treated separately because (a) they are not usually closely associated temporally, and (b) the behavior preceding and following copulation is usually peculiar to those contexts.

In the literature on ducks, many people use "courtship" interchangeably with "social courtship" (see below) to refer to the activity that occurs when groups of...
swimming birds gather together and perform displays. One difficulty with this definition is that use of the word "groups" seems to exclude interactions related to pair-bonding that involve only one male and one female (called "nuptial courtship" by Hochbaum 1944; "directed courtship" by von de Wall 1965; "pair courtship" by Cramp and Simmons 1977, and many other authors). In this paper, I will use "courtship" as a general term to refer to activities associated with the formation, testing, and maintenance of pair-bonds or liaisons. It includes both "social courtship" and "pair courtship."

The terms "pair" and "pair-bond" will be used to refer to a special relationship between one male and one female that has spatial, temporal, and interactional features peculiar to mates. These characteristics have been noted by many authors (e.g., Hochbaum 1944; Weidmann 1956; Lebret 1961). The most important criteria used to identify "paired" birds are: (a) mates maintain close proximity to one another, though the effort expended to do so may be one-sided; (b) pair-bonds persist for some time, usually weeks, months, or years; (c) mates frequently show cooperation (e.g., in parental care, nest building, resource defense); (d) mates preferentially or exclusively direct certain behavior (displays, copulation) toward one another; (e) mates actively protect their relationship by behaving aggressively toward rival specifics. It should be noted that the terms "pair" and "pair-bond" (and others such as "attachment," "affiliation," and "attraction") are used in different ways by different authors (see especially the general discussions by Wickler 1976 and Erickson 1978, and the recent studies by Anderson 1984, 1985, and Bluhm 1985).

Most waterfowl form pairs and the primary mating system is monogamy, in the sense of the social relationship described above (see chapter 6 of this volume). In some species, polygynous relationships occur (most often bigamous bonds), and in some basically monogamous species, paired males engage in extra-pair courtship that can lead to mate switches for subsequent nesting attempts (Anderson, 1985). The term "liaison" has been used when a paired male has a secondary part-time relationship with another female (McKinney et al. 1978), although some authors (e.g., Black and Owen 1988) reserve this term to refer to an early, tentative stage in pair formation with a primary mate. I will use it here to refer to a part-time bond of either kind. Males of many basically monogamous species engage in forced extra-pair copulations; in the best-studied species these are paired males, and extra-pair copulations are evidently secondary male reproductive strategies (McKinney et al. 1983; Afton 1985; Ewars and Williams 1987). Therefore, pair-bonding is a social relationship that may or may not involve exclusive paternity of the female's clutches by her mate (see chapter 6).

Social courtship (= Gesellschaftsspiel [social play], Heinoth 1911; also called "flock display," Dane and van der Kloot 1964; "social display," Raitasuo 1964; Weidmann and Darley 1971; "communal display," Cramp and Simmons 1977) has been a frequently discussed topic of controversy in the duck literature, as reflected by the many terms used for it. I will use "social courtship" because this is a particularly well-established term, and I believe that it encompasses a variety of activities that are related primarily to the formation and maintenance of liaisons and pair-bonds. This view is controversial, however, and it is necessary to review briefly the history of ideas on social courtship to understand the controversies.

B. History of Ideas on Social Courtship

Heinoth (1910) believed that male ducks gather around females to show themselves off by performing displays as part of the process of competing for mates. This interpretation of social courtship has been accepted, at least in general terms, by many subsequent observers, because it seems to make sense in relation to the activities of the birds. Males appear to compete for the attention of females by orienting their displays toward them, and females show preferences for certain males while rejecting others.

Seasonal changes in behavior provide additional support for the view that pairs are formed, at least in part, through social courtship. For example, in migratory Northern Hemisphere dabbling ducks, social courtship is first seen in the fall or early winter when few females are paired. It continues during the following months, and gradually more and more females become paired (Bezzel 1959; Lebret 1961). Late in the pairing season, the intensity of courtship increases as males compete more aggressively for the attention of the remaining unpaired females. The timing of these changes varies between species in association with the timing of pairing chronology, but the overall pattern supports the view that social courtship is related to pair formation.

Several apparent inconsistencies with this view were noted in studies on urban populations of Mallards by Weidmann (1956), Lebret (1961), and Raitasuo (1964). They discovered that (a) pairs can be seen before social courtship starts in fall, (b) social courtship continues in late winter when virtually all females are paired, and (c) many urban Mallards rejoin their mate of the previous year apparently without engaging in complex courtship activities. Most surprisingly, (d) paired as well as unpaired males were observed to participate in social courtship. Therefore, social courtship did not appear to be simply a mechanism for forming pairs, and other explanations were sought.

Weidmann (1956) and Raitasuo (1964) suggested that
social courtship has psychosomatic effects in stimulating gonad growth and arousing the urge to pair in females. Lebret (1961) believed that males use courtship displays such as the grunt-whistle to compete for mates, but he argued that the occurrence of social courtship gatherings after most pairs have formed requires a different explanation. He proposed that social courtship serves as a "canalizer" of aggression between males during the winter months when pairs are forced to live in flocks.

These samples from the literature of the 1950s and 1960s show that explanations for social courtship were frequently sought in terms of motivational effects and group selection arguments were common. The studies by Lehrman (1955, 1964) on hormone-behavior relationships in Ring Doves (Streptopelia risoria) were very influential at that time, and psychosomatic effects of courtship were believed to be widespread in birds. Subsequent studies on ducks (Desforges 1972, Bluhm 1984), however, did not confirm the stimulatory effects of male courtship displays on females that Raitasuo (1964) envisaged. Such effects are perhaps more likely in species with irregular breeding seasons, where birds begin courtship in response to rainfall or rising water levels and start egg-laying as soon as 10 days thereafter (e.g., Grey Teal in Australia, Frith 1959; Braithwaite 1976), but the role of courtship in stimulating gonadal development has yet to be demonstrated in such species. It is difficult to imagine that this could be the primary function of social courtship in ducks in general, because of the great length of the courtship period in many species (e.g., about 7 months in Mallards). Perhaps "pair displays" are involved in synchronizing the reproductive cycles of mates after a pair-bond has formed, as might be expected from results on other avian species (Wingfield 1980; Moore 1983) and as Bluhm (1984) suggested for Canvasbacks.

In recent years, attention has shifted away from earlier ethological approaches to social courtship. Trivers (1972: 150) encouraged this trend by pointing out that there is more to courtship than "allowing the individual to choose the correct species and sex, to overcome antagonistic urges and to arouse one's partner (Bastock 1967)." Emphasis on conflicting interests of individuals has stimulated research on tactical aspects of the behavior of individual birds. This avoids the tendency to view social courtship as a communal affair with a benefit to the group as a whole, an idea that had flavored many earlier discussions of the phenomenon.

C. Contexts of Social Courtship

The "selfish individual" viewpoint has fostered fresh ideas on old problems. Are males and females primarily assessing the qualities of potential mates while they maneuver and interact during social courtship bouts? When paired males join in social courtship, could they be assessing opportunities for alternative or secondary mates? Do females really have the final say in choosing mates, or could aggression between rival males be the crucial factor at times?

An especially important consequence of this perspective is that it dispels the idea that "social courtship" is a unitary phenomenon with a single functional explanation. From the point of view of the individual birds that participate, their "interests" are likely to be quite different depending on their sex, status (paired, pairing, unpaired), and previous experiences. This means that the processes involved cannot be teased apart without understanding the factors that determine the short-term and long-term "goals" of individual birds. We need to know what each bird is "trying to achieve" in its social interactions. Furthermore, it is possible that these processes are not the same in each of the tribes of ducks that perform social courtship. Initially, one way to approach the problem is to consider, in very general terms, the probable goals of birds with different status.

Unpaired birds. One process that must be involved in social courtship is competition among unpaired males for the establishment of pair-bonds. This does not mean that bonds can be established only through participation in social courtship, because several workers (e.g., Krujft et al. 1980) have pointed out that bonds can form in captive ducks without male courtship displays being given. But, if there is active competition among several males for one female, the result is a "courting party" (Hochbaum 1944). This is a group of birds in which the female is the center of attention, with males jockeying for position to perform attention-getting displays to her while interacting in competitive ways with one another (e.g., threatening, chasing). This is the simplest and most easily understood situation in which courtship displays are given. It is especially familiar to observers who have paid most attention to the later stages of the pairing season, when the intensity of competition among the remaining unpaired males is vigorous (e.g., Hochbaum 1944).

Few studies have been made on the early phases of pairing in wild populations, but it appears that there is much testing going on at this stage and the first liaisons to form are tentative and liable to change (Weidmann 1936, for Mallard; Whishart 1983b, for American Wigeon). This exploratory pairing behavior is reflected in observations of males moving around and directing displays at different females.

Mate-defense situations. Pair bonds in some Anas species appear to re-form in late summer so that from the beginning of the courtship season some paired birds are present in the wintering flocks. When such females are courted by unpaired males, they are likely to be rebuffed by the female (by inciting displays) and the paired male
may threaten them away also. This triangular relationship can produce situations in which courtship displays are given, not only by the unpaired male but by the paired male also.

Extrapair courtship and bond reaffirmation. Paired males of certain species have been observed to leave their mates temporarily to engage in extrapair courtship of other females (Weidmann 1956; Lebret 1961; Raitasuo 1964; McKinney 1975, 1985; McKinney and Stolen 1982; Stolen and McKinney 1983; Anderson 1985; Sorenson, in press). If the courted female is paired, the result is likely to be a bout of courtship in which both males direct displays to the same female (as in the mate-guarding situation described above). If the philandering male's mate then joins the group, he will switch and orient his displays to his own mate. This can lead to "social courtship," in which all participating birds are paired to other birds in the group. The directing of displays to his mate by the philandering male appears to represent a "reaffirmation" of his pair-bond, and this occurs frequently in species such as the White-cheeked Pintail (Sorenson, in press) and Canvasback (M. G. Anderson, pers. comm.) in which males are especially active in extrapair courtship.

It is possible that mate-holding tactics of paired females can also bring about situations in which "social courtship" occurs. Competitive behavior between females was observed in bigamous Cape Teal and Speckled Teal (Stolen and McKinney 1983; McKinney 1985). This took the form of enticement to copulate by incubating females, vigorous inciting beside the male with threatening toward the rival female, and overt aggression between the females. Such interactions can attract the attention of other birds, thereby creating situations in which males perform displays.

Many observers (e.g., Weidmann 1956) have noted that disturbances of various kinds can trigger social courtship. For example, if a resting group of Mallards in a city park is mildly disturbed by dogs or people walking close to them during the fall or winter months, the birds are likely to fly or swim out from shore a short distance and social courtship begins. Similar incidents are common when new birds alight and the groups mix. Perhaps these situations provide favorable opportunities for males to direct displays at females that interest them and, for other individuals, to reaffirm bonds.

Male-male interactions. Lorenz (1941) reported that at times male Mallards perform courtship displays in the absence of females, and von de Wall (1965) concluded that the presence of females is of minor importance in the social display of this species. On the other hand, Johansgard (1960a) emphasized that the female plays a major role in Mallard social courtship (notably in promoting the synchronization of male displays), and Weidmann and Darley (1971) showed experimentally that the introduction of a female (but not a male) to a group of males elicits social courtship. The latter findings, on the central importance of the female, have generally been accepted, and there has been a tendency to dismiss the earlier records of male-only courtship groups as abnormal events, perhaps byproducts of male-male homosexual relationships (Schutz 1965a). However, in recent mate-choice experiments with wild and domestic Mallards, Krujt et al. (1982) found that pair-bonds often formed in the absence of social courtship displays by males and that social displays were "often performed, though at a lower frequency, by males in the absence of females." This finding was supported in another study of urban Mallards (Bossema and Roemers 1985: 153) in which a trio (2 males, 1 female) was observed. In this trio, the males were intense rivals because the female showed attachment to both of them by her inciting behavior. In the absence of the female the rivals directed "courtship" displays (grunt-whistle, head-up-tail-up) to one another, but when she joined them both males directed most of their displays to her.

Observations on captive and wild White-cheeked Pintails (McKinney et al. 1990) have revealed that males use the down-up (the main display from the Anas repertoire used by this species) both as a courtship display (in male-female contexts) and as a threat display (in male-male hostile situations in the absence of females). Similar multiple use of the grunt-whistle and bridling displays by male Speckled Teal was recorded, and many of the hostile contexts were associated with intense rivalries between the males concerned. Examples of multiple use of displays can be found in the literature on various other waterfowl (e.g., Aythyni, Mergini, Oxyurini), but the extent to which it occurs in Anas species remains to be seen. The possibility that the displays differ in details of their form, orientation, or associated behavior in the two situations also needs to be examined carefully in future studies.

D. Mate Choice and the Pairing Process

1. Effects of Early Experience

It has been recognized for many years that early experience can have important influences on the preferences of individual waterfowl for mates of a certain type. Lorenz (1935) drew attention to this phenomenon, now referred to as "sexual imprinting." It is well known to aviculturists because captive birds can easily become imprinted on the "wrong" species or sex (e.g., Immelmann 1972). For example, if a male Mallard duckling is allowed to grow up without exposure to a female, it is likely to be homosexual in its attachments as an adult and will show no interest in courting females. Similarly, males of many waterfowl species can be sexually im-
printed on females of species other than their own by raising them together.

Lorenz (1935) distinguished this phenomenon from the process, now termed "filial imprinting," whereby newly hatched ducklings and goslings develop a preference for following their mother. Lorenz was especially impressed by the rapidity of these learning processes, their operation during restricted "critical periods" in the bird's life, and their irreversibility. Imprinting attracted the interest of many researchers, and there is now a large literature on the topic (see reviews by Klinghammer 1967; Hess 1973; Bateson 1966, 1978; Immelmann 1972; Sluckin 1972; Smith 1983).

Pioneering research on sexual imprinting in waterfowl was carried out at Lorenz's institute at Seewiesen by Schutz (1965b). By raising birds of different species together, Schutz concluded that birds develop preferences for pairing with members of the same species but not with the specific individuals they were raised with. He found that the sensitive period for sexual imprinting was from 3 to 9 weeks of age, in contrast to filial imprinting, which occurs within the first day or two after hatching. Experiments indicated that it is easier to imprint to a foster mother than to a foster sibling. Supporting Lorenz's claim for the irreversibility of imprinting, Schutz found that some of his interspecific pair-bonds lasted for many years.

Of special interest was Schutz's finding that in sexually dimorphic species (e.g., Mallard, North American Wood Duck, Muscovy), only males were imprinted. He concluded that "females are almost incapable of becoming imprinted, as they react innately to the releasers of the male courtship dress." Schutz believed that, in dimorphic species, females respond innately to males of their own species but males require imprinting ("a special form of plastic and precise learning") to enable them to recognize correctly females of their own species that have inconspicuous plumage with few distinctive species-specific features. Schutz's experiments with Speckled Teal, a monomorphic species where both sexes have inconspicuous "female-like" plumage, indicated that females were just as easily imprinted as males. Schutz's work was followed up by Lannoy (1967), Sherrod (1974), and Klint (1975, 1978, 1980), the main focus again being on plumage color. From his extensive experimental work with Mallards, Klint (1980) concluded that initial mate choice of females is dependent on male plumage features and that this preference is innate.

Recent studies have not supported the conclusions drawn by Schutz and Klint, however, and their studies have been criticized on the basis of faulty experimental design and the behavioral criteria used to detect preferences. In experiments with wild-type and domesticated white Mallards, Bossema and Krujìt (1982) showed that regardless of the color type of the males, females paired with males that courted them most intensively. Experiments with different Mallard strains carried out by Cheng et al. (1978) and Krujìt et al. (1982), in which females were allowed to express their preferences without interference from competing males, clearly showed that females preferred males of the type they had been reared with. Similar preference tests by Brodsky et al. (1988), using Mallards and North American Black Ducks, confirmed this result. Therefore, in tests where females are allowed to interact freely, dominant males keep subordinates away from females, and so females tend to pair with dominant males.

These studies of dabbling ducks lead to several important conclusions: (a) early experience can greatly influence mate choice preferences of both males and females; (b) females make their choice from among those males that court them most actively; (c) competition between courting males and the resulting dominance relationships can be important in determining which individuals eventually pair. Also, these studies have drawn attention to the need for careful experimental design and caution in drawing conclusions from experimental manipulations. These points, and related questions about sexual imprinting, are more fully reviewed by Immelmann and Suomi (1981), Bateson (1981), and ten Cate (1985).

2. The Process of Pairing

The behavior involved in pair formation has been described in several waterfowl species, although usually a picture of the overall process has been pieced together from observations (often on unmarked individuals) at various times during the pairing period. Such descriptive accounts have been given for Anas species by Weidmann (1956), Bezzel (1959), Johnsgard (1960a, d), Lebret (1961), von de Wall (1963), Soutiere et al. (1972), McKinney et al. (1978), Wishart (1983a, b), Hepp and Hair (1983), Paulus (1983, 1988), and Brewer (1991). Work on captive dabbling ducks by Weidmann and Darley (1971), McKinney (1975), Schommer (1977), Goldsmith (1979), Laurie-Ahlberg and McKinney (1979), Dervieux and Tamisier (1979), Cheng et al. (1978, 1979), Standen (1980), Bossema and Krujìt (1982), Krujìt et al. (1982), Williams (1982, 1983), Bossema and Roemers (1983), and Brodsky et al. (1988) has added greatly to our knowledge of the pairing process. Research on pair formation in other waterfowl tribes is less extensive, but the studies by Fischer (1965) on Greylag Geese, Weller (1965, 1967) on Redheads, Afton and Sayler (1982) on American Goldeneyes, Armbruster (1982) on North American Wood Ducks, Bluhm (1985) on Canvasbacks, and Owen et al. (1988) and Black and Owen (1988) on Barnacle Geese are noteworthy.

Pair formation is likely to entail at least four tasks for both males and females. These are (a) demonstrating in-
terest in a particular individual, (b) attracting and holding this individual’s attention, (c) establishing and strengthening a pair-bond relationship with the selected individual, and (d) countering interference from competing rivals. Conceivably much of the behavior involved in the preliminary testing of willingness to pair could be subtle, inconspicuous, and difficult to detect, but little is known about these aspects. Perhaps under demonstrative behavior is to be expected when individuals that know one another well reuni e after a separation. When strangers are involved, however, assessment and bonding are likely to require adjustments on the part of both birds, and because the outcome is uncertain, the interactions may be expected to last for a considerable period of time (e.g., at least several days).

Much of the behavior observed in courting ducks can be interpreted as accomplishing the four general tasks of specifying interest, attracting attention, fostering relationships, and countering rivals. For example, in courting parties of Anatini, Aythyini, Cairinini, and Mergini that include a group of males following one female, it is obvious that the female is the focus of the males’ activities. They constantly show their interest in her by trying to get near her and by directing displays to her. Females respond in various ways to the males, for example, by giving calls in response to male displays, by performing displays that attract and stimulate courting males, and by threatening certain males. Males maneuver in attempts to induce the female to follow them, and females indicate their preference by giving inciting beside one male. Males jockey for position, threaten one another, and engage in chasing and fighting. (The roles of displays in these activities are discussed in more detail in II.F.)

Birds in the process of forming bonds show several kinds of behavior indicating that they are adjusting to, and presumably also assessing, one another. They begin to synchronize their activities, so that their bouts of feeding, preening, and sleeping coincide, and by means of preflight signals they ensure simultaneous takeoff. They copulate, call to another and reunite if separated, and perform special displays that seem to reaffirm their attachment to one another (e.g., inciting by females, preen-dorsal, preen-behind-wing, belly-preen by males in many Anas species). In these ways, both male and female appear to strive actively to strengthen the relationship. Thereafter, as long as the bond survives, at least one member of the pair can be seen to initiate bond-maintenance activities and protect the mate from takeover by rivals. Bouts of joint displays (e.g., triumph ceremonies) are frequent in species where male and female collaborate closely in territory defense and/or brood rearing.

The importance of competition between males during pairing in wild populations of ducks is especially apparent late in the season when most females are strongly paired. In courting parties, many males crowd tightly around certain females, jockeying for favorable positions from which to direct displays or trying simply to remain at the female’s side. Fights between males are frequent. In contrast, early in the pairing season, social courtship activities of many species are more slowly paced and competition between males is more subtle. Studies of particular species have shown that the aggressiveness and competitive skills of males are essential to successful pair formation (e.g., Wishart 1983b), and that the ability of paired males to continue to thwart challenges by rival males can be vital in maintaining pair bonds (e.g., McKinney et al. 1978). In general, these factors are likely to be very important in all waterfowl species.

The inevitable conflicts involved in forming and maintaining pair-bonds are especially vivid in species that exhibit extrapair courtship and bigamy. Such situations highlight the potential for competition between females for exclusive pair/bond relationships. This aspect deserves more attention because male-male competition is usually emphasized in the literature on pair-bonding in ducks.

The events leading to pair formation in geese are difficult to study because they take place in wintering flocks and bonds probably develop slowly. In Barnacle Geese, Black and Owen (1988) distinguished four chronological phases in pair formation: (1) “mate-searching” by unpaired males entails walking through a flock while adopting distinctive postures; (2) “herding” occurs when a male locates a female and persistently follows her, apparently trying to separate her from the rest of the flock; (3) “mock attack” involves an aggressive run toward other geese that stops short of attack and is followed by a triumph ceremony performed with the prospective mate; (4) “prolonged triumph ceremonies” are mutual performances by male and female, performed by new pairs before and after the male makes a series of real attacks on other geese. The process of pair- ing appears to be similar in other geese (Fischer 1965; Raveling 1970) and triumph ceremonies are also very important in pair formation in swans (Kear 1972).

3. Mate Choice Criteria

No aviculturalist would question the generalization that waterfowl assess potential mates and make choices among them. It is general practice in zoos and collections of captive waterfowl to allow pairs to form naturally in flocks and to select the most strongly bonded pairs for propagation. Attempts to force the process by selecting a male and a female at random and placing them alone in a breeding pen are often unsuccessful. This has been convincingly demonstrated by Bluhm (1985) in experiments with captive Canvasbacks.
Williams (1982) provided experimental evidence showing that different female Mallards were consistent in preferring certain males when given a choice, and many observers have noted that male ducks show strong preferences for courting particular females while ignoring other unpaired females in the vicinity (Weidmann 1956; Bezzel 1959; Lebret 1961; Wishart 1983b; Sorenson, in press). Therefore, it is likely that active mate choice, by both males and females, is a general phenomenon in all anatid tribes.

In recent years there has been a great deal of interest in the phenomenon of mate choice and its implications for the theory of sexual selection (Campbell 1972; Bateson 1983a; Bradbury and Andersson 1987). Waterfowl are of particular interest in this regard because most migratory species form pairs away from the breeding grounds so that quality of breeding territory cannot be used as a criterion for selecting a breeding partner (McKinney 1985, 1986). Choices must be made solely on the basis of morphology and/or behavior of the birds themselves. Many suggestions have been made about factors that are likely to be involved in mate choice by waterfowl (Williams 1982, Anderson et al. 1988), but firm evidence can come only from experiments and few studies of this kind have been made. A major problem is that both male-female competition and female choice are likely to occur at once, and it is difficult to separate the two effects.

Familiarity should be mentioned first, because many waterfowl are known to have strong tendencies to remain paired with, or to re-pair with (= "reuniting" in Rowley's 1983 terminology), the same partner for repeated breeding attempts. Important advantages to be gained by collaborating with the same mate (e.g., increasing reproductive efficiency with age and experience, saving of time needed for courtship, physiological compatibility of partners) have been reviewed by Rowley (1983), and many of these factors could apply to waterfowl. In species with prolonged parental care by both parents (swans, geese, whistling ducks), the needs for synchrony, complementarity, and compatibility in the collaborative activities of mates are especially important (Erickson 1978) and the advantages of long-term (in many cases lifelong) pair-bonds are increased. Even in certain species in which mates are able to separate during postbreeding migrations and pairing occurs thereafter during winter (e.g., European Shelduck, Patterson 1982; European Eider, Spurr and Milne 1976; Barrow's Goldeneye, Savard 1985), surprisingly high rates of reuniting of pairs between seasons have been documented. In many migratory species of Anatini, Aythyini, and Cairinini, however, reuniting may not occur (e.g., Canvasback, Anderson 1985) or it may occur rarely (e.g., Mallard, Dwyer et al. 1973; Seymour 1991). High annual mortality rates may be an additional factor reducing the likelihood of mates reuniting in some of the latter species. In sedentary populations of ducks opportunities for reuniting to occur are likely to be much greater (e.g., Moulton and Weller 1984; Sorenson, in press).

In spite of the advantages of re-pairing with the same mate, there are situations in which it will be to an individual's advantage to switch mates (e.g., if one bird becomes sick or injured). Also, during renest intervals and during the courtship season in species with seasonal pair-bonds, there are presumably situations in which individuals must choose between the options of reuniting or switching mates. The factors influencing such decisions are difficult to study, and little seems to be known about the processes in any waterfowl species.

Early experience is known to be very important in influencing preferences of both male and female Mallards for a mate of a particular species, sex, and "type" (notably similar to the parent, siblings or domestic strain of the "rearing group") (see III.D.1). The criteria involved in such discriminations and the processes whereby preferences are formed remain mysteries. Probably they are "much more complex and subtle than was supposed by the classical view of imprinting" (Kruifj 1985). The relative importance of morphological features, vocalizations, and behavioral actions in shaping these preferences is not clear.

An important question concerns the possibility that natural selection has promoted mechanisms of inbreeding avoidance. Bateson (1983b) argued that animals may be expected to strike an optimal balance between inbreeding and outbreeding when choosing a mate, and he presented evidence that sexual imprinting is one mechanism whereby "optimal outbreeding" is achieved. His experiments with captive Japanese Quail (Coturnix coturnix) indicated that sexual preferences are finely tuned by their early experience with birds of the opposite sex; after being reared with siblings, most quail preferred a first cousin over a sibling or an unrelated individual. Bateson suggested that sexual imprinting could be a learning process resulting in a reduced responsiveness to both novel (unrelated) and familiar (related) individuals. Thus, rather than being a mechanism that promotes pairing with a member of the correct species (which was the original view), sexual imprinting may operate as an "optimal outbreeding mechanism."

Of course, other factors operate in most waterfowl populations that must influence the level to which inbreeding occurs (e.g., sex differences in dispersal patterns and wintering areas, intraspecific brood parasitism, multiple paternity of clutches), and it is not clear whether a mechanism such as Bateson proposes could, or would, be expected to evolve. Preliminary experiments with Mallards (Williams 1982) and North American Black Ducks (C. C. Blohowiak, pers. comm.)
indicated that sib-sib pairings can occur among captive-reared birds, and there was no evidence of tendencies for individuals to avoid them. Further experimental research is needed to investigate whether there are influences of genetic relatedness on mate preferences.

*Morphological features* are known to play a role in mate choice decisions in certain species. In the polymorphic Lesser Snow Goose, mate preferences are greatly influenced by plumage color, white × white and blue × blue pairings being much commoner than mixed pairs (Cooke and McNally 1975). There is also evidence that body size is a factor in this species (Ankney 1977; Cooke and Davies 1983).

Choice experiments with captive Mallards have indicated that quality of male plumage is an important factor in initial female mate preferences (Klint 1980; Williams 1982; Holmberg et al. 1989; Weidmann 1990). In some of these experiments, male plumage features (red breast, black curving tail feather, white tail) were altered or removed, but possible confounding effects of dominance rank of the males were not avoided.

Age undoubtedly influences mate choice, even in species that are capable of breeding when 1 year old. Cues that waterfowl use in discriminating between birds of different age have not been studied, although age differences in such likely features as eye color (Trauger 1974) and display performance (Korschgen and Fredrickson 1976) have been documented. Body size and condition, plumage and soft-part features, and behavior could all be involved. In any event, old experienced birds evidently have substantial advantages over yearlings in competing for mates. This is reflected in the high proportion of young male dabbling ducks that fail to obtain mates during their first pairing season (e.g., Blohm 1982; Wishart 1983b; Sorenson, in press).

*Male dominance rank* has been shown to be very important in female preference tests in captive Mallards (Williams 1982; Bossema and Roemers 1983; Brodsky et al. 1988). Although these experiments showed that females pair with high-ranking males, it is difficult to tell whether the females were actively choosing dominant males or if dominant males were sequestering the females. High-ranking males dominate the situation in competitive courtship tests, giving them advantages in attracting and holding the female's attention. In earlier experiments with captive Mallards, Goldsmith (1979) thought that male dominance relations sometimes changed before the female indicated her switch in preference, but in other instances the female's preference seemed to change first and the switch in male dominance relations followed. Such impressions are difficult to evaluate, however, and the relative importance of male-male interactions and female preferences remains uncertain.

*Courtship motivation and abilities* are likely to be important in mate choice, but it is difficult to separate these characteristics from body and plumage condition, age, dominance status, and experience. Male Mallards showing high courtship activity and persistence were preferred by courted females in experiments with captives (Cheng et al. 1979; Bossema and Kruith 1982; Kruith et al. 1982; Holmberg et al. 1989), and males that position themselves in front of the female while performing displays (e.g., Head-up-tail-up) seem to have an advantage (Weidmann and Darley 1971). Courtship behavior of subadult males is known to differ from that of adults in various ways. For example, the displays of subadult male American Goldeneyes are more variable and not as precisely oriented as those of older birds (Dane and van der Kloot 1964), and similar differences have been noted in dabbling ducks (Kaltenhauser 1971) and North American Wood Ducks (Korschgen and Fredrickson 1976). Presumably, courtship skills improve through experience.

Although it appears that bonds can form in isolated "pairs" of captive Mallards without the performance of male courtship displays (Kruith et al. 1982), and pairs can reunite without courtship, this may be because displays are of minor significance in the absence of male-male competition. Their main roles appear to be in enabling individuals to assess potential mates, compete for the attention of females, persuade females to respond, and deter rivals. Therefore, it should not be concluded that courtship displays are of little significance in the natural processes of pairing.

A topic for comparative study is the possible relationship between the cues that males and females use in evaluating potential mates and the characteristics of mates that will be most important later, during the breeding season. In American Wigeon, for example, Wishart (1983b) has suggested that females may be expected to assess males on their attentiveness and aggressiveness during winter courtship because these are the characteristics that will be most important in providing protection for the female and securing the breeding territory. He also noted that group flights and attempts at copulation during courtship in this species could enable individuals to assess the flying ability and agility of potential mates. In this regard, females might be expected to prefer agile males primarily because of their need for effective mate guarding during forced copulation attempts, while males should prefer agile females that are likely to be able to elude males, thereby reducing the risk of cuckoldry. These are intriguing ideas, but inherently very difficult to test.

*Competence in copulation* is logically an essential ability of a mate and there is circumstantial evidence that waterfowl use this to help assess potential mates. Copulations have been recorded in many duck species throughout the pairing season, often several months be-
fore eggs are laid (e.g., Cramp and Simmons 1977). Although these “winter copulations” could be serving several functions (e.g., practice, strengthening bonds), it is difficult to imagine that they have no relevance to mate assessment (Afton and Sayler 1982).

IV. Diversity of Signal Systems

Earlier reviews of waterfowl display repertoires emphasized taxonomic implications (Delacour and Mayr 1945; Johnsgard 1961a), evolutionary trends within the family (Johnsgard 1962), and descriptive accounts for each species (Johnsgard 1965). More comprehensive and up-to-date summaries of the behavior of the best-studied species can be found in the handbooks by Bauer and Glutz (1968, 1969), Palmer (1976), and Cramp and Simmons (1977), and updated but brief accounts for the whole family are presented in Johnsgard (1978). In this section, I discuss ecological and social factors that appear to have shaped signal systems. This approach, based on the ecological correlation method pioneered by Crook (1964), may provide some insights into the evolution of signals by generating hypotheses on their adaptive features.

Crook’s three-step conceptual model proposed that, during the adaptive radiation of families such as the weaver birds, ecological factors have molded the social system of each species (see chapter 6 of this volume), and social systems in turn have shaped communication methods. Although ecological factors (e.g., habitat structure) can influence communication methods directly, it is primarily through the social system that the signaling needs of individuals are determined. Therefore, specific variations in signal systems within a group cannot be understood without a thorough knowledge of the social system of each species.

This approach entails the search for (a) correlations between differences in the display repertoires of closely related species and differences in their social systems, and (b) similarities in the signals of distantly related species that can be explained by ecological or social factors that they share (convergent evolution). There are many difficulties inherent in this approach (McKinney 1978), and in spite of recent refinements in comparative methods, interpretations are usually tentative (Jarman 1982; Ridley 1983; Clutton-Brock and Harvey 1984; Gittleman 1989; Harvey and Pagel 1991).

A major problem with ecological correlation is that detailed profiles of species-typical behavior are needed for each species and often these are based on one study, carried out on one population at one time. Intraspecific variations in social behavior are now widely recognized in many animal groups (Lott 1984), and the study of alternative mating strategies is currently an active field of research (Krebs and Davies 1987). Although a large liter-
including calls (called "concerts" by Davies), may correspond to triumph ceremonies of anserine geese. They are first seen in goslings, where they appear to include the "begging call" performance, and are associated with aggressive behavior as well as parental feeding. In adults, concerts often occur during or following a bout of threatening, and during pair formation.

Aggression is frequent in flocks when one family approaches another. Males attack more often than females. Breeding pairs are highly territorial, and males do most of the defense. Davies described the "uplift call" of territorial males as a series of honks delivered from an alert posture with an uplifting of the open bill as each note is given. These calls are given by males when other geese fly over or land near their families, and are often followed by an attack. A male will give similar calls if he becomes separated from his family; then the family members reply and reunite.

Thus, in spite of its special features, the signal repertoire of the Magpie Goose has much in common with the repertoires of anserine geese. In view of their distant relationship, it is possible that these similarities are results of convergent evolution in birds with similar lifestyles. This possibility could be investigated by further detailed comparative study.

B. Dendrocygnini

The nine species of whistling ducks comprise a widely distributed tribe of tropical ducks. They are gregarious, nocturnal or crepuscular, and primarily vegetarian in diet, but there are striking specific differences in habitat preferences and feeding methods. Some wade and graze and may nest far from brood-rearing waters (Dendrocygna eytoni), others are highly aquatic and dive for most of their food (D. bicolor, Thalassornis leuconotus), and one species frequently perches in trees (D. autumnalis). Pair-bonds are believed to be long-term, both sexes incubate, and biparental brood care is the rule.

Conspicuous behavioral features of these birds are their specifically distinct whistling calls. They call frequently, especially in flight, presumably to keep contact with mates and family members. Heinroth (1911) drew attention to the peculiar shape of the outermost primary of D. javanica, which makes a whistling noise in flight, and he suggested that this enables birds to keep in contact during flight.

Distinctive mutual postcopulatory displays are similar throughout the group, but the behavior associated with pair formation is evidently subtle and has not been carefully studied in any species. There are interesting possibilities in this group to relate signal repertoires to specific differences in lifestyle and habitat characteristics. Sonograms of duckling distress calls are figured by Kear (1968) and calls of adult D. eytoni are presented by Frith (1982), but there is no detailed description of the vocalizations of any species. Group threatening performances by families (e.g., Black-bellied Whistling Ducks) need special attention because of their superficial resemblance to those of aggressive goose families. The highly aquatic White-backed Duck—apparently a whistling duck that has adopted an oxyurid lifestyle—is the most extreme specialist in the group, but as yet has been little studied.

C. Anserini

Signaling needs of swans and geese have been influenced greatly by the grazing lifestyle, long-term pair-bonds, and prolonged parental care. Flocking during the non-breeding season is favored by the need to exploit patchily distributed, renewing food supplies, and by the use of open environments. Terrestrial grazing exposes geese to danger of surprise attack by both terrestrial and aerial predators. Therefore, vocal signals that give warning of danger, keep mates and families together as cohesive units, and allow separated birds to find their mates or families again are frequently heard from grazing flocks. The vocal repertoires of the Greylag Goose and Canada Goose have been especially well studied (reviewed by H. Fischer and E. Fabricius in Cramp and Simmons 1977). In species such as the Canada Goose, visual signals involving head and neck motions are used instead of noisy vocalizations during the gosling phase, when parents are flightless and long overland movements may be required, and families need to avoid drawing attention to themselves (Black and Barrow 1985).

In wintering flocks, competition for access to good feeding sites among individuals, pairs, and families entails the use of combined visual and vocal displays comprising "threat codes," used to establish and advertise dominance status (e.g., Raveling 1970). Especially important in this respect are various forms of triumph ceremony (see II.F.3), which are also components of the pair formation process in geese (Black and Owen 1988). During the breeding season, territorial pairs of many swan and goose species advertise their territories with triumph ceremonies involving conspicuous wing-waving movements and loud bouts of calling (Kear 1972; Aksesson and Raveling 1982). Mute Swans use mechanical sounds made by clapping the feet on the water to advertise their territories (Lumsden 1985; Black 1986); neighboring rivals also perform nonviolent rotation displays while threat posturing at territorial boundaries (Lind 1984). Although some anserine species are nonterritorial and breed in colonies (e.g., Black Swan), most species in this group show high levels of overt aggressiveness associated with competition for breeding territories or nest sites.
D. Cereopsini
The Cape Barren Goose is one of Australia’s distinctive waterfowl. It shares morphological and behavioral features with both anserine geese and sheldgeese, but is sufficiently distinctive to be given separate tribal status. It is a sedentary and highly terrestrial grazer with greatly reduced aquatic habits; even copulation occurs on land. Pairs are very aggressive and territorial during the breeding season. The female collaborates with her mate in nest defense, and mates perform a triumph ceremony that occurs throughout the year. The young participate in triumph ceremonies with their parents. Descriptive accounts of the behavior of captives have been published (Veselovsky 1970; Pells 1982), but information on social organization and signaling in wild populations is incomplete (see Marchant and Higgins 1990).

The displays of the Freckled Duck are of special interest because of the light they may shed on the taxonomic relationships of this unique species. In a recent study, however, Fullagar et al. (1990) reported that there are no conspicuous pre- or postcopulatory displays and the pre-flight neck-stretching is not distinctive. The only male display appears to be the axle-grind. It is usually directed toward a female but it may also reflect aggression toward other males. The male’s head is thrust forward as soft creaking sounds (a buzz followed by a brief squeak) are uttered, and the display ends with a vigorous tail-wag. The female responds with head-raised chin-lift accompanied by a throaty chuckle. Jonsgard (1965b) suggested that these displays might correspond to a triumph ceremony. Fullagar et al. (1990) point out that the structure and rhythm of the calls in the axle-grind display show some similarities to certain advertising displays of oxyurids, notably those of the Black-headed Duck, but homologies have not been established with confidence.

E. Stictonettini
The South American sheldgeese are primarily terrestrial grazers and most are large-bodied birds. They are generally viewed as ecological counterparts of the nearctic anserine geese. Pairs are territorial and very aggressive during the breeding season, both parents cooperate in rearing the young, and they live in flocks during the non-breeding season. Long-term (perhaps often lifelong) pair-bonds and prolonged parental care have been documented in the Upland Goose (Summers 1983) and may be characteristic of the whole group.

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triomp ceremony), the male adopts imposing postures with head held back and chest pushed forward and gives a series of high-pitched whistling calls while the female walks around him keeping her head forward or lowered and gives bursts of much deeper, harsh calls (Fig. 7-2). The male Andean Goose has a bizarre threat display in which the head is rolled on the back and the wings are opened to reveal brightly colored patches on the carpal area where spurs that are used in fighting are located. Signaling has not been studied intensively in any of these species.

Shelducks combine grazing and dabbling feeding methods and, like sheldgeese, pairs are territorial and very aggressive; most show striking sex differences in plumage. They differ from sheldgeese in having a period of parental care; families break up when adults leave the breeding area to move to safe locations for the wing molt. The same pairs often reunite in winter flocks, on spring staging areas, or on the breeding territory in successive years, but mate switches also occur and rivalry over mates and territories is intense (Williams 1979; Patterson 1982). Pairing anew before each breeding season appears to have favored the evolution of more complex courtship repertoires in this group than in any of the groups discussed above.

An especially intriguing aspect of shelduck courtship is the major role played by females. As described originally by Heinroth (1911), females have highly developed inciting and this display apparently stimulates one male to attack a rival male. Competition between females for mates is evidently very strong in several shelduck species, presumably associated with unusual female-biased sex ratios (see chapter 6 of this volume). Williams (1979) has studied pairing in wild Paradise Shelducks and describes the process as follows. In the winter flock, temporary liaisons are common. During inciting, which is the main female display, the head points forward and loud, rapidly repeated, high-pitched calls are given continuously. In this posture the female points at the bird
she is threatening while swinging her head from side to side, and then she often charges. Meanwhile the male she is associating with moves close alongside her, adopts a high-and-erect posture and gives loud single honks or rapid series of double-syllabled notes while pivoting first toward the threatened bird and then back to his mate. The male then adopts a head-low threat posture and charges. Following a successful chase, the pair engage in a mutual trumpeting ceremony, and then the male switches to a disyllabic “triumph call” and makes rapid upward jerks of the head. The success of the male in these encounters with other birds seems to determine whether the pair-bond persists.

Territoriality is an especially important element of shelduck social behavior. Pairs are noisy and conspicuous during the breeding season, and their signals appear to be designed primarily to serve as deterrents to territorial intruders and sexual rivals. Loud, insistent calling and associated elaborate movements of head and neck are characteristic of territory owners. Signaling of this type seems well suited for long-distance communication in the open habitats that shelducks occupy.

G. Tachyerini

Steamer ducks of South America are large-bodied divers, named for their method of locomotion by wing-flapping across the water surface. Although often viewed as ecological counterparts of the eiders (genus Somateria), steamer ducks behave very differently (Weller 1976). They are highly territorial, pairs of the flightless forms apparently holding year-round territories along stretches of marine shorelines. These are all-purpose territories, used for feeding, nesting, and brood rearing, and they are defended against conspecifics through elaborate patrolling, threat displays, and damaging fighting involving the use of wing spurs. Furthermore, Flying Steamer Ducks show vigorous interspecific hostility (including killing) toward a wide range of species that trespass in their territories (Nuechterlein and Storer 1985; Livezey and Humphrey 1985).

During territorial encounters, pair members perform joint threat displays that include vocal duets (Nuechterlein and Storer 1985). These entail vertical pointing upward with the bill in the stretch display (with groaning calls) by the female, the short-high-and-breed display (Moynihan 1958) with cocked tail and wing spurs exposed (with rasping grunts) by the male, followed by more groants by the female superimposed on trill-like ticking notes from the male (Fig. 7-3). These displays advertise the pair's ownership of the territory and they are also given after attacks. Therefore they appear to be functionally equivalent to triumph ceremonies.

Weller (1976) drew attention to some similarities between the short-high-and-broad and the bubbling display of the North American Ruddy Duck. Both entail a cocking of the tail with exposure of white undertail coverts. It may be no accident that Tachyeres and Oxyura, among the most exclusively aquatic genera within the family, both use tail cocking, one of the most conspicuous actions possible for a swimming bird.

An interesting suggestion with respect to the adaptive significance of interspecific aggression, and killing in Tachyeres was made by Nuechterlein and Storer (1985). They observed that a female often appeared to instigate a fight between her mate and other conspecific individuals, and because females are often present during interspecific aggression, they proposed that possibly males victimize other species in order to display their
belligerency and tightening abilities to their females."
There are intriguing parallels here with the traditional
interpretation of what is going on during inciting in
shelducks.

H. Cairinini
The perching duck tribe includes a diverse array of spe-
cies, mostly tropical, many of which are placed in
monotypic genera because they seem not to have close
differences with other living species. They have sharp
claws for perching, elongated tails for maneuvering in
flight through wooded terrain, and most prefer to nest
in tree-holes. Perhaps the most famous member of
the group is the Mandarin, remarkable for its spectacular
male plumage and highly developed social courtship.
Lorenz (1941) suggested that the male's orange "sail
feather" has evolved specifically as a visual reinforcer
for the highly ritualized preen-behind-wing display. This
interpretation is still generally accepted, and it earns the
Mandarin a place in most ethology textbooks.

Relationships between the signal system of the Comb
Duck and its arboreal habits have been discussed by
Siegfried (1978). Harem polygyny appears to be charac-
teristic of this species, and males have a spectacular
wing-flap display that they use to threaten rivals and
attract females. This display is often delivered from tree-
top perches and, as with other courtship display
postures of males, the signaler orients his body laterally
to the recipient. Siegfried noted that changes in body
posture involve "slow, deliberate bowing and sideways-
stepping movements" that seem particularly suitable for
signaling while perched precariously on a branch. Simi-
larly, the fighting technique of males, which involves
striking blows with the wings rather than pecking and
biting, may be associated with arboreal habits. These
ideas might well apply also to the displays of other
members of this tribe, for example, the Mandarin, in
which side-by-side body orientations of mates (as on a
tree branch) are appropriate for delivery of ritualized
preening displays and tactile signaling via mutual
preening.

In general, the calls of male perching ducks are quiet
wheezes and whistles given at close range, while those of
females are loud and seem effective over longer dis-
tances. Members of this tribe (e.g., Aix species) are es-
pecially active in twilight periods and some have
communal nocturnal roosting habits. These characteris-
tics of the Cairinini lifestyle may have had widespread
influences on signaling methods. In the Ringed Teal, for
example, the wings of both sexes make a distinctive
whistling noise during flight and they also have loud
contact calls, all presumably associated with the need
for mates to keep each other informed about their
whereabouts in woodland habitats and in poor light
(Brewer 1987).

The Australian Maned Duck is unique in the tribe in
being a terrestrial grazer. The display repertoire does not
appear to have been greatly affected by this change from
an arboreal lifestyle such as that of its presumed closest
relatives, the two species of *Aix*. Kingsford (1986) has
drawn attention to the frequent use of female inciting in
grazing flocks, where it appears to be very commonly
directed at conspecific individuals of both sexes. More-
ever, in this species, the threatening component of incit-
ing appears to be used in a variety of contexts (e.g., by
a female with her brood), and (as in *Aix*) very similar
actions are performed by males. It would be interesting to
compare the level of aggression between pairs and fam-
ilies in grazing Maned Ducks with that in dabbling
flocks of *Aix*; perhaps the frequent inciting of Maned
Ducks is associated with a high level of feeding competi-
tion, as occurs in grazing geese.

The social courtship activities of Mandarins have
many parallels to those of dabbling ducks, raising inter-
esting questions concerning how these two groups have
solved similar signaling problems. While it is possible
to classify the displays of *Aix* and *Anas* were present
in a common ancestor of the two groups (e.g., turn-
back-of-head, preen-behind-wing, inciting), it seems
likely that some similarities have resulted from conver-
gent evolution. Like those of *Anas* species, the male at-
tention-getting displays of *Aix* are performed with
deliberate orientation of the whole body or the head in
relation to the focal female. The single and double dis-
play shakes are similar to the grunt-whistle, while the
wing-and-tail-flash is reminiscent of the head-up-tail-
up, but neither Lorenz nor Johnsgard views these simi-
larities as indicating homologies. Differences in the
signal repertoires of the two genera also occur. *Aix*
males perform a rapid, single vertical chin-lift (exposing
the white throat) directed both toward rival males and
until females they are courting; *Anas* males seem to
have no counterpart, and the rapid, multiple chin-lifting
of female wigeon is quite different. *Aix* females have no
vocalizations corresponding to *Anas* decrescendo calls,
and no *Anas* females have calls resembling the coquette
call of *Aix*.

Although many of the male courtship displays of *Aix*
are spectacular movements that show off special plum-
age structures, they are designed for short-range signal-
and the accompanying vocalizations are muted. In con-
trast to the large-bodied waterfowl discussed above,
the signal systems of small-bodied ducks like the *Aix*
species appear to reflect the vulnerability of these birds
to diverse kinds of predators. None of the small perching
ducks is territorial, and in general they are quiet and
inconspicuous in demeanor. Unobtrusive behavior may
be favored because of the high risk of surprise attack by
predators in woodland habitats. This suggests that in-
volved in elaborate social courtship gatherings may

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be especially hazardous for these species. The possibility that this factor has influenced courtship display repertoires has not been explored.

I. Merganettini

The Torrent Duck is a river specialist with a unique behavioral repertoire. Eldridge (1979) has given the most detailed description of the signals, and she had difficulty detecting any homologies with the displays of other anatids. In the vertical-shake the bird flips a spray of water droplets at another bird with its bill, but the form of the movement is quite different in details from that of the Anas grunt-whistle or the ritualized shakes of Aix and Tadorna. This display is performed by both sexes during hostile encounters between pairs and it is also given by males in the precopulatory context. This indicates a multipurpose display, because the orientation of the performer’s body is lateral to the target bird and the water drops are precisely aimed at the other bird in both types of situation. The mule-kick is given by both sexes during hostile interactions, the performer usually facing away from its opponent and directing a spray of water backward with both feet. Body-bend displays are also performed by both sexes and in various situations. All three of these displays are usually performed while the bird is swimming, but they can also be given from a perch on a rock.

An interesting aspect of these displays is that they involve bursts by, or flexing of, both legs simultaneously—actions that could have been derived from hopping. Unlike other anatids, Torrent Ducks frequently use hopping. They hop in a similar way as penguins do, to get out of the water on to a rock, or to move from one rock to another. The water-kicking displays of oxyurids also entail simultaneous movement of both legs, but the leg actions are quite different and they do not propel the bird’s body vertically out of the water.

Torrent Duck display actions and vocal duets are evidently very important in the joint defense of territories by mates. Territoriality, joint defense by mates, and damaging fighting using wing spurs occur in two (probably three) other river dwelling ducks but, although there are similar needs for combined threatening and pair-bond reinforcement, the display repertoires of all of these species are distinctive. One way in which the Torrent Duck differs is in the apparent use of the wing spurs as visual signals, exposed during hostile displays. Torrent Ducks seem particularly well adapted for life in white-water rapids, where the physical demands of river life are most severe. One factor, stressed by Eldridge (1979), is the need for vocalizations to carry over the background noise of the torrents, and this appears to apply particularly to the piercing whistles given by males of this species and other river ducks.

How do Torrent Ducks succeed in raising ducklings in such a hazardous environment? Little is known about the roles of males and females in brood care, and no studies have examined how signals may be modified to enable parents and ducklings to communicate.

J. Anatini

The dabbling ducks comprise the largest tribe within the family. In some ways this is the most uniform tribe, in that most species are judged to be congeners (genus Anas), and not unexpectedly they share many displays. On the other hand, this group of ducks is quite diverse in the habitats exploited and lifestyles adopted. One reason for the successful radiation of dabbling ducks appears to be the basic body build of these birds. They have a flexible, multipurpose feeding apparatus, and they are accomplished in the use of all four methods of locomotion open to ducklike birds—walking, swimming, diving, and flying. This allows many species to be flexible in their ecological requirements (unlike stifftails or geese). They are good generalists and thus have exploited most kinds of wetland habitats, while some species show secondary specialization for certain restricted foods or habitats.

Associated with their generalized locomotory abilities, dabbling ducks have diverse signal repertoires including displays specialized for use while swimming, walking on land, and flying. Many species have courtship, including long display chains, copulatory activity often continues when groups walk out on shore or take wing. The seven major subgroups within the genus Anas (wigeons, green-winged teals, austral teals, pintails, mallards, silver teals, and blue-winged ducks) appear to represent major lines in the adaptive radiation of the group. Each subgroup has distinctive plumage and soft-part features and certain distinctive behavioral characteristics (e.g., wigeons are grazers with goose-like bills; blue-winged ducks strain surface plankton and have bills with many lamellae). These subgroup specializations appear to have shaped display repertoires to some degree. For example, many blue-winged duck displays are derived from aquatic feeding methods frequently used by these birds (McKinney 1970).

Specific variations in display repertoires within each Anas subgroup present interesting problems, but so far only a few species have been studied in detail with the possibility of ecological correlations in mind. The African Black Duck (A. sparsa) has an unusual repertoire that can be interpreted as a consequence of specialization for river life (McKinney et al. 1978). The opportunity to apply this method is particularly good in this case, because there is convincing evidence that sparsa is a member of the mallard subgroup and that it adopted river life as a secondary specialization. This provides a firm working hypothesis on the direction of evolutionary change, so that differences in the behavioral reper-
toire between sparsa and other living mallard species can be linked to the change in lifestyle.

Specialization for river life appears to favor strong development of territoriality (see chapter 8 of this volume). Sparsa pairs hold exclusive, all-purpose territories, only territory-holding pairs can breed, and mates must collaborate in defense if territories are to be held. This appears to have selected for aggressiveness in both males and females (pairs use wing spurs as weapons for fighting) and for strong pair-bonds. A major consequence of the territorial system is that social courtship (well developed in the mallards) no longer occurs and the major mallard courtship displays (grunt-whistle, head-up-tail-up) are rarely used. On the other hand, mutual greeting displays occur frequently between mates, apparently serving in both territorial defense and bond reinforcement.

Another river specialist, Salvadori’s Duck, is also known to be territorial on rivers in New Guinea (Kear 1975), but its display repertoire has not been examined in detail. Better known is the repertoire of the New Zealand Blue Duck (Eldridge 1983). Although the affinities of this species are debatable, and it may not belong in the Anatini at all, there are interesting similarities to the other river species that seem likely to have evolved convergently as adaptations to a linear territorial spacing system. Thus, as well as engaging in territorial battles using wing spurs, male Blue Ducks have a piercing whistle that carries well over the sound of rushing water, and pairs have mutual displays that are used as joint threats during territorial encounters.

Further opportunities to trace evolutionary changes in display repertoires are presented by the island forms of dabbling ducks. In many cases, the ancestral mainland species from which these forms are derived can be inferred with confidence, and changes in behavior can be related to factors associated with colonization of island habitats. Although several island races or species have retained complex male courtship repertoires, the island forms of Anas aucklandica, presumed to be derived originally from the Australian Chestnut Teal (A. castanea), show notable changes. The Chestnut Teal occurs mainly near the coast in south and west Australia, where it prefers brackish coastal lagoons, estuaries, and creeks, and in Tasmania, where it is found on inland swamps and lakes as well as coastal wetlands. The New Zealand Brown Teal (A. aucklandica chlorotis) has retained a similar preference for brackish, coastal wetlands, especially tidal creeks and adjacent waterlogged terrain, but it has adopted quite a different lifestyle (Weller 1974; Hayes and Williams 1982; Dumbell 1986). During the nonbreeding season, Brown Teal occupy communal daytime roosts at traditional sites on tidal reaches of streams; they move out from the roosts at dusk, and feed during the night on nearby boggy land. They are extremely aggressive birds; males are territorial during the breeding season and roosting birds are very quarrelsome. While Chestnut Teal have a mainly vegetarian diet, Brown Teal consume mainly invertebrates.

Field observations have revealed striking differences between the display repertoires of the Brown Teal and Chestnut Teal (Williams et al. 1991). In the Brown Teal, grunt-whistles are performed singly, rather than linked in display chains with other displays; head-up-tail-up and down-up appear to be absent from the adult courtship repertoire, occurring only as relics in juveniles; jump-flights and courting flights are either rare or absent; chains of ritualized comfort movements (e.g., bill-dips, preen-dorsal) are very common during courtship.

The changes in the signal system that evidently took place when the Brown Teal stock evolved could have been influenced by a number of factors. For example, the extreme aggressiveness of these birds (presumably associated with territoriality, biparental brood care, and perhaps the invertebrate diet) may reduce the effectiveness of long chains of conspicuous attention-getting displays that are liable to be disrupted by rival males. The use of more subtle displays derived from comfort movements may be less provocative to rivals, and it could be more suited to the Brown Teal lifestyle because they can be performed equally well on land and water. The absence (or rarity) of aerial courtship patterns is presumably associated with highly terrestrial habits. Modifications of visible and vocal displays for crepuscular and nocturnal signaling might also be expected in this species.

K. Aythynn

Although the pochards share some displays with the dabbling ducks (e.g., turn-back-of-head, preen-dorsal), most species have a set of distinctive male courtship displays unique to the tribe. These are the kinked-neck call, neck-stretch, head-throw, and sneak displays, all of which entail postures in which the head and neck are moved in characteristic ways by birds swimming on the water surface. Similarly the postcopulatory bill-down posture involves only the head and neck, and it also occurs in all members of the tribe. Although the head-throw is a spectacular display with obvious attention-getting qualities, none of the pochard displays seems to entail the flipping of water that occurs in several other duck tribes. Most male vocalizations are relatively quiet mewing noises, while the main female calls tend to be louder and harsh in quality.

Social courtship is similar in general form to that of dabbling ducks, except that there are underwater chases as well as courting flights. The repertoire of Aythya species is well illustrated by Weller’s (1967) description and photographs of courtship in the Redhead. In courting...
parties with usually one female and several males, the males compete for a position close to her (often vigorously) and perform displays with marked orientation components in relation to her. Some displays (e.g., sneak) are used in both courtship and threat contexts, and threatening and chasing by the female as well as the males can be frequent. Mutual displays (neck-stretch, drinking), presumably serving as pair-reinforcing signals, are frequently performed by pochard pairs. Anderson (1983b: 244) suggested for Canvasbacks that this might be related to their habit of diving, especially in flocks, where mates constantly become separated and are often very close to other birds. Frequent extrapair courtship, well documented in the Canvasback by Anderson (1984), might also be a factor promoting these displays. In some pochard species the male performs an aerial tail-pull as he flies behind his mate. Female inciting has two alternating components, a threatening pointing toward the rejected bird and neck-stretch toward the mate. Female pochards are notably aggressive toward males other than their mate, and females play very active roles in pair formation and pair-bond maintenance.

Two members of the genus Netta have somewhat different display repertoires. Rosy bills are surface feeders rather than divers, and they spend more time courting on land than other members of the tribe. Highly ritualized forms of the sneak and drink displays are striking in this species, but factors that could have favored these developments are not obvious. The Red-crested Pochard is also less exclusively a diver than are the Aythya species, and it is more agile on land. Males have most of the Aythya displays but lack the head-throw, and social courtship is more like that of dabbling ducks in having a stereotyped “introductory” phase (Lind 1962; summarized in Cramp and Simmons 1977). A particularly frequent male display is the sideways sneeze (probably a homologue of the kinked-neck call of Aythya), in which the bill points downward, the ruffled crest is pointed toward the female, and a rasping wheezing call is given. In courtship context this display is almost always preceded by a head-flick. When used as a threat display toward other males there is no head-flick.

Pair-bond behavior of the Red-crested Pochard is especially interesting because it includes courtship feeding, in which the male dives and brings up vegetation that his mate consumes on the surface. This behavior has not been reported in pairs of other waterfowl. It is not known whether courtship feeding plays a significant role in providing additional food for breeding females, or if its function is symbolic in pair-bond reinforcement. In any case, the factors promoting its use in this particular species are intriguing.

L. Mergini

Most sea ducks have complex signal repertoires, but because of the diverse species included in the tribe homologous displays can be identified only in the case of some congeners. Detailed summaries are provided for most species by Cramp and Simmons (1977).

Social courtship occurs primarily on water and is well developed in this tribe. Many species have courting flights and/or underwater pursuits. Male vocalizations are particularly diverse (e.g., cooing of eiders, bugling of Long-tailed Duck, whistling of scoters, buzzing of goldeneyes). Several species (e.g., goldeneyes) produce a winging noise during flight. Although some swans, whistling ducks, perching ducks, and dabbling ducks also produce wing noises, foggy conditions common in coastal marine habitats may have favored frequent use of this type of continuous, audible signal in sea ducks (A. Reed, pers. comm.). Similar wing noises are made by both sexes of the Black Scoter, but the deeply emarginated outermost primaries of males are presumably involved in producing the louder wing noises that accompany courtship display flights.

The display repertoire of the Common Goldeneye has been well studied, most recently by Afton and Sayler (1982), who paid special attention to the signal functions of displays. Several striking male displays (mastehead, fast head-throw-kick, slow head-throw-kick) are given frequently by courting males and appear to have attention-getting functions. The head-forward is performed as the male faces directly at another bird it is likely to attack. The mastehead, which begins and ends in a posture very similar to the head-forward, is usually performed lateral to the female; Afton and Sayler suggest that it could be serving as a multipurpose display—as a threat toward males and as an attention-getting signal to the female. Short display flights are oriented away from the female and their attention-getting quality is reinforced by wing noise. These flights seem designed to entice the female to follow the male and, if they succeed, copulation may follow.

The precopulatory behavior of sea ducks is different from that of most species in other tribes in that the female assumes the prone posture and holds it for a considerable time (up to several minutes) while the male swims beside her performing displays. The details of the male precopulatory display repertoire vary from species to species, but ritualized comfort movements are most common. There tends to be a sequence of displays through which the male proceeds as the moment of mounting nears; certain displays are frequent early in the sequence, others appear for the first time late in the sequence, and often the final displays are fixed. The overall impression is that the female is receptive from the start but that the male must go through a preparatory
procedure before mounting. The male's delay in mounting and the changes in his display sequence suggest that changes in male motivation or physiological state are involved.

In the Common Eider, male precopulatory display sequences are particularly complex and the relative frequency of the different displays varies with circumstances (McKinney 1961: 55). Some of these variations are associated with the male's age, the approach of other birds, or the strength of the male's sexual motivation. It seems unlikely that each display could be transmitting a specific message to the female; perhaps changes in the content of the male's display performance provide information on his overall motivation that is monitored by the female. The puzzling point is that the female appears to be receptive throughout, and she does not make obvious changes in her posture in response to the male's displays. Interpretations in terms of conflicting male tendencies or male arousal and self-stimulation are not very convincing, because they fail to explain why the male needs to keep the female informed via such an elaborate series of signals. Why do sea ducks follow this pattern instead of the mutual precopulatory display patterns of most other anatids?

Another puzzling phenomenon associated with copulation in sea ducks is the performance of one or more wing-flicks by the male while he is mounted. This has been recorded in certain Melanitta, Bucephala, and Mergus species; in some species it is a regular component of precopulatory behavior, in others it occurs sometimes. The significance of these movements (or the sound they produce) is unexplained.

The lengthy nature of copulatory sequences in sea ducks, along with the generally open-water habitats used by these birds, may make pairs vulnerable to surprise attack by aerial predators. Although most sea ducks are sociable during the winter and prebreeding seasons when copulations occur, it is necessary for pairs to separate themselves from other birds to avoid interruption during their long copulation sequences. In small-bodied species such as Steller Eider the risk of attack from eagles and falcons appears to have promoted extreme gregariousness during winter, and pairs are reluctant to leave the flock. This vulnerability seems to have had repercussions on the pattern of copulation behavior (McKinney 1965b). Pairs fly out from the flock to copulate, and return promptly thereafter; unlike Common Eiders, males do not use the conspicuous ritualized wing-flap and shake displays throughout their sequences, nor do they give loud calls. In these, and other respects, the precopulatory repertoire of Steller Eider appears designed to reduce the duration of sequences and the conspicuousness of the birds, thereby minimizing the risk of surprise attack. This interpretation is strengthened by a comparison of the courtship display repertoires of these two eider species. A strong tendency to fly (e.g., in aerial flock maneuvers when a raptor is sighted) appears to have favored the use of preflight displays and short flights in Steller Eider courtship. These are absent in Common Eider courtship, and are replaced by underwater pursuits and complex, conspicuous display actions accompanied by loud cooing calls.

M. Oxyurini

The stiffness have many unique features and attempts to use behavioral characters to deduce relationships to other anatid tribes have not been successful. One recent view is that the group diverged very early indeed in the family's history, and that its closest affinities are with the Anserini and Dendrocygini rather than with the duck tribes now included in the Anatinae (see chapter 1 of this volume). Morphological adaptations of the stiffness for diving (Raikow 1970, 1973) are associated with their almost entirely aquatic habits (see Siegfried 1976). They live in deep-water marshes, feeding mainly by sifting invertebrates from the bottom mud. Most species occupy warm temperate climatic zones and the Southern Hemisphere species tend to have sedentary populations. Stifftails build platforms in emergent vegetation for nest sites and resting places, and, at least in some species, both sexes actively build (Siegfried 1973). Parental care is not highly developed: males are not known to participate in brood care in any species and ducklings are self-reliant at an early age. One species, the Black-headed Duck, is an obligate brood parasite and ducklings grow up completely independently.

The mating systems of oxyurids are not well understood, but in general pair-bonds are weakly developed and several species are promiscuous (see chapter 6 of this volume). This has placed a premium on male advertising abilities. As Siegfried (1976) pointed out, there are dramatic differences among oxyurid species (notably Maccou Duck and Ruddy Duck) in the degree to which males behave territorially. The Musk Duck may be the most territorial of all; males approach lek species in their reliance on male advertisement to attract females for mating. Much descriptive, comparative work has been done on the distinctive display repertoires of stiffness (Johnsgard 1966, 1967; Matthews and Evans 1974; Siegfried and van der Merwe 1975; Hays, in Palmer 1976; Johnsgard and Nordeen 1981; Carbonell 1983; Fullagar and Carbonell 1986), but most emphasis has been on taxonomic relationships within the group.

Functional aspects of signaling systems have been discussed in detail by Siegfried and van der Merwe (1973) and Siegfried (1976). These authors reasoned that since oxyurids are relatively small birds and they inhabit waters with dense emergent vegetation, visual communica-
tion frequently is effective over short distances only. The bright blue bill of males is thought to be an important visual reinforcer of frontal threat postures. H. Hays (in Palmer 1976) describes how it is concealed in the Ruddy Duck by being buried in the scapulars (as in the sleeping posture) apparently as an appeasement display. Also, in the Ruddy Duck the white undertail coverts are exhibited during tail-cocking in which the male swims away from, and in front of, the female as though "leading" her.

Male oxyurids depend primarily on sound production for long-distance advertising. The sounds they produce are distinctly different from other marsh noises and well suited for communication through emergent vegetation. Unlike the mechanisms of vocal sound production found in other anatids (involving convoluted windpipes and tracheal bullae, Johnsgard, 1971), stifflists combine vocal and mechanical methods in unique ways. For example, in the Bubbling display of the male Ruddy Duck, the bird raises its head and inflates the tracheal air sac, slaps the bill downward on to the chest 6 to 12 times (thereby making a clapping sound, creating bubbles in the water around the breast by forcing air out of the breast feathers), and then, as the neck is stretched forward, a two-syllabled call, "raa-anh," is uttered. In another distinctive display of this species, the ring-rush, the male rushes across the water while beating his wings, the feet making a ringing sound as they propel the bird across the surface (Hays, in Palmer 1976). Head movements involved in some displays function to inflate air sacs for sound production, as explained by Siegfried and van der Merwe (1975) in their description of the vibrating trumpet call display of the Maccua Duck.

Even more bizarre postures are involved in the paddle-kick, plonk-kick, and whistle-kick displays of the male Musk Duck (Fullagar and Carbonell 1986). The advertising function of these displays is clearly shown by their repeated performance in prolonged bouts (up to 20 minutes, nonstop). The tail is cocked completely forward over the bird's back, the head is stretched forward with throat sacs inflated, and the feet kick in unison producing plonking noises and creating conspicuous water splashes on the sides. An extremely loud, piercing whistle is emitted during most of these displays.

The long-distance sound signals of male oxyurids are no doubt perceived, and reacted to, by both males and females. Their primary function probably is to attract females for mating, but with variations in body orientation and associated display movements, some of them are used in both threat and courtship contexts. For example, in the Maccua Duck, a display used to advertise the territory to rival males (independent vibrating trumpet call) differs in several ways when used in courtship contexts. In the Ruddy Duck, bubbling is used both as a threat toward other males (performed facing the rival) and as a courtship display (performed broadside to the female).

Frith (1982) reported that the musky odor of the male Musk Duck derives from the uropygial gland and that it becomes much more intense during the breeding season. This suggests that the odor may function in mate-attraction, but this possibility has not been investigated.

V. Future Research Needs

A. Research Strategies and Methods

Prior to 1970, most studies of courtship and communication in waterfowl focused on displays. The display repertoires of different species were described, their great diversity was revealed, and homologies were sought because they proved to be useful taxonomic characters. This comparative, taxonomic approach was productive, but it had limitations. For example, most attention was paid to displays associated with social courtship and copulation because these proved to be most useful taxonomically, and display descriptions were often cursory because presence or absence of homologous displays was of most interest. Specific differences in display repertoires were revealed, but they were assumed to be arbitrary conventions resulting from selection for behavioral isolating mechanisms. Ecological influences were rarely considered.

In the past 20 years, many of the approaches that were characteristic of classical ethology (e.g., seeking homologies) have been replaced by quite different research strategies. Key concepts from sociobiology and behavioral ecology are now taken for granted—the primary importance of selection at the individual level, conflicts of interest between males and females, analysis of behavior in terms of costs and benefits, and the influences of ecological factors in shaping social systems. Predictions derived from evolutionary theory are now used as the basis for research programs, and alternative hypotheses on the adaptive functions of behavior are tested systematically. The topics of courtship, pair formation, and signaling are central to questions of great interest to behavioral ecologists, and researchers studying these facets of waterfowl behavior need to be aware of current theory in this discipline.

Social tactics of individuals and the manipulative potential of displays are likely to be major areas for future research. The "selfish signaler" approach will be challenging, however, because it calls for so much information about the study population. In many cases, conflicts of interest may not be apparent until the overall social system, and the ecological factors that shaped it, have been thoroughly investigated. Social tactics may vary as social relationships between interacting individuals change over time. Therefore, to progress to a more so-
phisticated grasp of what is really going on during in-
teractions involving signaling, studies of displays should be
integrated into broad research programs on the behavior
and ecology of the study species. Similarly, comparative
studies that investigate ultimate factors producing dif-
fences in signal systems between closely related spe-
cies, or convergence in the signals used by distantly
related species, require information on the behavioral
ecology of each species. A good example is the interest-
ing problem of the factors that have promoted the use of
formalized interactions in many different kinds of
waterfowl.

Farabaugh (1982) concluded that vocal dueting in
birds has evolved independently in many groups, and
that its use is correlated with year-round territoriality,
prolonged monogamous pair-bonds, and occurrence in
the tropics. Several species of geese were included in
Farabaugh's review (she considered triumph ceremonies
to be duets), but other species of waterfowl also have
different displays and her review could be extended.

Well-developed joint ceremonies that conform to
Farabaugh's criteria for "dueting" apparently occur in
Maggie Geese, probably all swans and anserine geese,
Cape Barren Geese, probably all shelducks, sheldgeese,
and steamer ducks, Torrent Ducks, Blue Ducks, African
Black Ducks, and wigeons. Most of these waterfowl do
defend breeding territories (in some cases year-round),
and many of them are known to have prolonged monog-
amous pair-bonds. Migratory geese do not hold year-
round territories, but they do stay in family groups
during winter, pairs and families compete as units in
wintering flocks, and the principle of "strength in num-
bors", applies. As Farabaugh suggested, this may be
functionally similar to the year-round territory situa-
tion. Two potential functions of joint ceremonies—
combined threats, and promotion of cohesion in pairs
and families—evidently apply in these geese. The impor-
tant role of mock attacks and subsequent triumph cere-
momies between potential mates during pair formation
strongly suggests that they are assessing each other's de-
defensive behavior.

The "strength in numbers" principle may be of basic
importance in the other waterfowl that perform joint
ceremonies, but the degree to which such behavior op-
erates in territory defense apparently varies. Although
joint defense of territory by males is important in river
specialists and Steamer Ducks, the triumph ceremonies
of Chiloe Wigeon appear to function mainly in pair-
bond and family cohesion (Brewer 1990).

Comparative studies on factors that promote the use
of joint ceremonies would be valuable. Detailed analyses
are needed to detect variations in the form, frequency,
and vigor of joint ceremonies in various situations, and
in the degree of participation of the sexes in each species.
Differences in cost-benefit ratios of participating in cer-
emonies for males, females, and offspring, and changes
in these ratios over time, are likely to be important fac-
tors, but such information will be very difficult to ob-
tain.

In addition to research on functional questions asso-
ciated with behavioral ecology, other strategies will be
needed to investigate proximate causes of signaling be-
behavior. Studies of causation and development remain
the province of ethology, where the focus is on behavioral
rather than ecological levels of analysis (see Barlow
many refinements have been made in ethological meth-
ods (e.g., Wickstrom 1982; Martin and Bateson 1986).
These include new methods for studying causation at
both motivational and physiological levels (e.g., behav-
ioral endocrinology of wild birds studied in the field),
and improved techniques for testing hypotheses on prox-
imate functions of vocal signals via playback (Kroodsma
1989). New tools, such as high-definition video cam-
eras, now enable us to record and analyze behavior
more accurately, easily, and cheaply than was possible
using movie film. The video technique is especially valu-
able in research requiring repeated sampling of behav-
ioral events, as in developmental studies.

Current knowledge about communication in water-
fowl is highly variable in quality. Many of the published
accounts of display repertoires for single species are
based on unquantified observations of captive birds.
Few field studies have been made on how displays are
used by marked birds of known status, so understanding
of the signal systems is superficial. The processes of mate
choice and pair formation have been examined in detail
in very few species. Therefore, much basic observational
work is still needed; in the case of endangered species
the need is urgent.

Descriptive studies pose many problems. There is no
"ideal ethogram" and decisions on what to record, how
detailed the description should be, and how the findings
should be presented will vary depending on the objec-
tives of the study. Many scientific journals are reluctant
to accept descriptions of behavior, and researchers usu-
ally must justify descriptions by using them to define
problems or test hypotheses. For example, the need to
document the form and orientation of multipurpose dis-
plays (see section III.C) can be justified by the insights
provided by similar studies on gulls and terns (Beer
ful review of different methods used to describe and de-
pict displays and behavioral interactions in birds.

B. Evolution of Signal Systems

The development of improved phylogenies and new
comparative methods to test phylogenetic hypotheses
about behavior (reviewed by Gittleman 1989) promise
exciting possibilities for distinguishing effects of phylogeny versus function on signal evolution. More confident reconstructions of the detailed branchings in the family tree could lead to explicit hypotheses on speciation patterns within waterfowl tribes and new insights on the directions of evolutionary changes in signal systems.

New evidence on anatid phylogeny may help to resolve some long-standing problems regarding the importance of phylogenetic constraints in the evolution of social systems and breeding strategies. Johnsgard (1962) and Kear (1970) proposed evolutionary trends in various morphological and behavioral features (e.g., monomorphism to dimorphism, large to small body size, long-term to temporary pair-bonds, generalized to specialized nesting and feeding adaptations, biparental to uniparental care, simple to complex displays) based on comparisons among living waterfowl species. These proposals included assumptions about the timing and sequence of branching patterns, and of tribal radiations, during the evolution of the family. Development and testing of alternative hypotheses would be helpful.

Information derived from intensive studies on the behavior and ecology of single species is still necessary to develop ideas on how ecological factors shape social systems and how ecological or social factors shape signal systems. Comparative studies can complement such evidence by revealing patterns across species. The two methods are interdependent and both are sure to be important in future studies of behavior evolution.

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