THE MOBILITY OF BREEDING PINTAILS

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ABSTRACT.—During 1971, 1972, and 1973 the mobility of breeding Pintails (*Anas acuta*) was studied in the pothole region of central North Dakota. A total of 5 unpaired males, 8 paired males, and 15 females were marked and followed for periods long enough to enable home range estimation. The mean home range sizes for unpaired males, paired males, and paired females were 579 ha, 896 ha, and 480 ha, respectively. Males were generally more mobile than females at all stages of the reproductive cycle.

Mobility was found to vary with reproductive chronology, usually decreasing from the prenesting to the nesting period. Seven pair ranges that included both the prenesting and nesting period averaged 509 ha, while four pair ranges that included only the nesting period averaged 167 ha. Female mobility was found to be greatest during the period preceding laying, and home range estimates for the prenesting period were significantly larger than home ranges calculated for the laying period. Females that renested were found to have reduced mobility throughout the renest interval.

Home range estimates for breeding Pintails are generally larger than those previously recorded for other *Anas* species. Interspecific variation in breeding home range size is apparent, and reflects differences in social behavior and feeding ecology.—*Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, Minnesota 55455*. Accepted 20 September 1976.

THE spacing behavior of breeding ducks has received much attention in the literature. Hochbaum (1944) suggested that breeding ducks are territorial, each pair occupying and defending a particular area. Although the behavioral responses among breeding pairs and the seasonal timing of pursuit behavior support this view (McKinney 1965), the application of this concept to some species has been repeatedly questioned (Bezzel 1959, Lebret 1961, Hori 1963). Data obtained on pair mobility have shown specific differences in spacing patterns. While some species approach the classical territoriality described by Hochbaum, other more mobile species clearly do not (Sowls 1955, Dzubin 1955, McKinney 1965, Seymour 1974a, 1974b). Such specific differences in mobility and home range size are correlated with differences in feeding and social behavior and appear to reflect rather subtle differences in evolved breeding strategies (McKinney 1965, 1973, 1975).

Information on mobility and breeding home range size has been collected for many *Anas* species. Despite qualitative statements in the literature regarding Pintail (*Anas acuta*) mobility, only two references have provided limited quantitative data (Dzubin 1955, Drewien 1967). The present paper discusses the mobility and home range size of breeding Pintails. The data used in this analysis were gathered during an investigation of this species' social system.

STUDY AREA AND METHODS

The 93-km² study area is in west-central Stutsman County, North Dakota, approximately 10 km south of Medina. This area falls within the Coteau du Missouri, a physiographic region of dead-ice moraine resulting from extensive stagnation following late Wisconsin glaciation. Resultant topography consists of closely spaced low hills interspersed with numerous shallow basin wetlands. The climate, geology, hydrology and aquatic plant communities of this region are described in detail by Winters (1963, 1967), Clayton (1967), Eisenlohr (1969), Eisenlohr et al. (1968, 1972), Sloan (1972), and Stewart and Kantrud (1971, 1972).

The central 41 km² of the study area contains approximately 331 wetland basins. According to the classification of Stewart and Kantrud (1971), which is based on surface water permanence, approximately 10% of the wetlands are ephemeral, 33% temporary, 35% seasonal, and 15% semipermanent (Dwyer

1974). Tilled wetlands of unknown class, permanent wetlands, and several fens comprise the remaining wetland percentages. Although few basins have been drained for agricultural purposes, about 19% of the basins are tilled annually. Many of the temporary and seasonal wetlands are hayed during mid or late summer.

All the land within the study area is privately owned and is subjected to rather intensive agricultural use. Excluding wetland acreages, current land-use is approximately 60% cropland and 40% pasture and hayland.

Pintails were captured at baited shoreline sites using projection nets (Dill and Thornsberry 1950) and floating treadle traps (Thornsberry and Cowardin 1971). Upon capture, birds were marked with adjustable, back-mounted radio packages (Dwyer 1972) and/or nasal saddles (Sugden and Poston 1968). Transmitter circuitry design was similar to that described by Cochran and Lord (1963).

The positions of marked birds were determined by triangulation and/or visual sighting. Approximately one third of the recorded locations involved visual contact. All plotting was done on aerial photograph maps, and point locations were recorded using a superimposed ordinate grid system. Most locations were obtained between dawn and dusk.

In analyzing home range I relied upon the methodology of previous workers to facilitate cross-species comparison. Period and cumulative home ranges have been calculated according to the minimum area method of Mohr (1947). A more conservative estimate of the home range, or "primary range," was calculated according to the method of Gilmer (1971), which involves the elimination of all peripheral fix locations prior to home range calculation. A location was designated as peripheral if it was 0.16 km or more from any other location recorded on a different day. Other quantitative measures used to characterize home range and mobility were maximum length (cf. Dzubin 1955) and mean activity radius (Hayne 1949). To be included in the analysis of home range an individual had to have at least one fix for each of 15 consecutive days and a minimum of 20 fix locations.

RESULTS

A total of 20 adult male and 20 adult female pintails were captured: 8 in 1971, 23 in 1972, and 9 in 1973. Eleven of these birds failed to meet the minimum criteria for analysis, and one late-caught female was excluded because she joined a postbreeding flock soon after capture. The remaining 28 birds included 5 unpaired males, 8 paired males, and 15 females. The mean number of fix locations was 63 for unpaired males, 90 for paired males, and 93 for females; tracking times averaged 32 days, 52 days, and 45 days, respectively.

Breeding home range in waterfowl has generally been defined as the area occupied between the breakup of postmigratory spring flocks and the completion of breeding (Sowls 1955: 48, Dzubin 1955). In the present study not all birds were captured immediately after arrival or at the same reproductive stage, and measurements of home range were often more restricted. For males "home range" includes the area occupied from capture until departure from the study area, and for females the area used from capture until hatching, departure, or postreproductive flocking.

Several pairs captured early in the breeding season typically spent most of the day on the study area, but moved 11 km or more to rejoin large flocks for night-time roosting. Such locations were not considered as part of the normal breeding home range and were subsequently omitted from home range analyses after breeding status was determined. Inclusion of these locations would have more than tripled the home range size of several pairs. Similarly, telemetric locations of questionable quality and locations that were noted to be the result of aerial pursuit activity were deleted prior to home range calculation.

Home range and mobility of unpaired males, paired males, and females.—Home range and primary range estimates varied considerably between individuals. I originally thought that much of this variation was due to individual differences either in the duration of tracking or in the number of recorded fix locations, but neither home
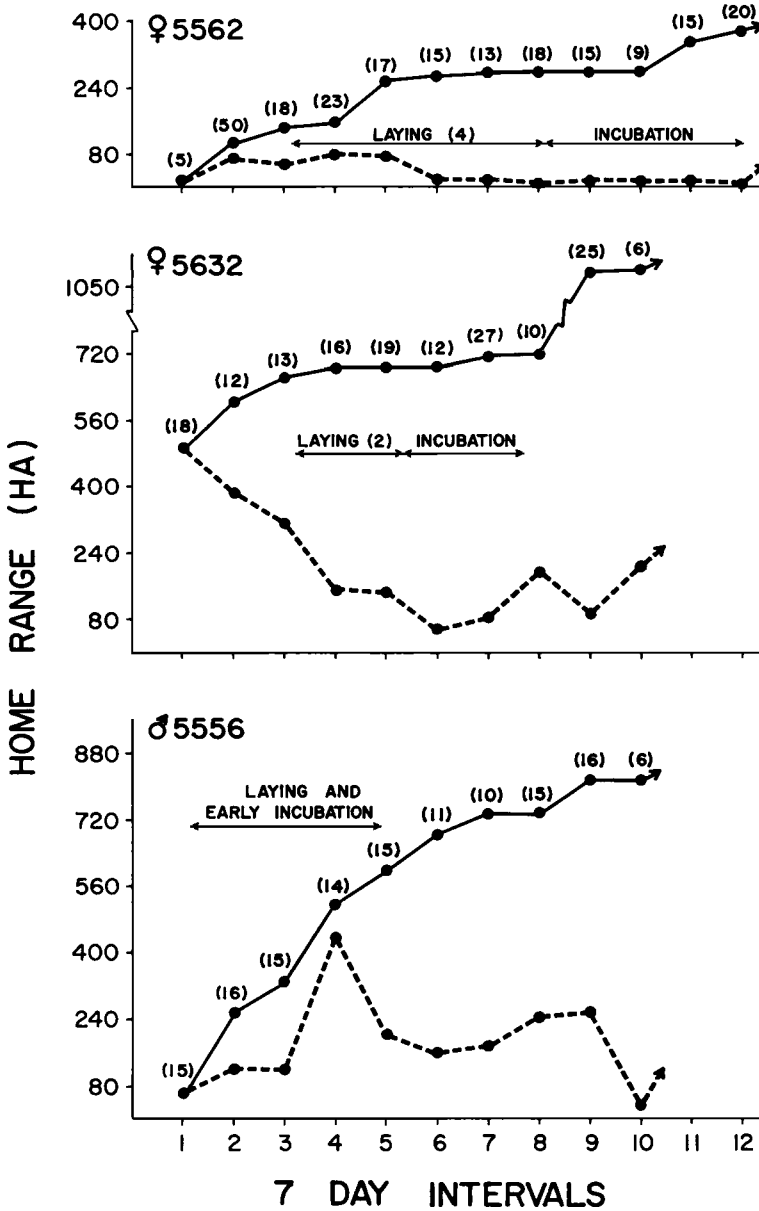
Fig. 1. Relationship between breeding chronology, cumulative home range, and period home range for three individual pintails. Solid line represents cumulative home range and the dotted line period range. Numbers in parentheses above the solid line represent the number of locations in each interval. Numbers in parentheses on the breeding chronology line represent number of documented nests.

range nor primary range estimates correlated significantly with either of these factors.

Home ranges and primary ranges tended to be largest among paired males, intermediate among unpaired males, and smallest among females (Table 1). Differences between the means for paired and unpaired males and for unpaired males and females were not significant, but the differences between the means for paired males

TABLE 1

COMPARISON OF HOME RANGE AND PRIMARY RANGE CHARACTERISTICS IN UNPAIRED MALE,
PAIRED MALE, AND FEMALE PINTAILS

Home range measurement	Unpaired males N = 5	Paired males N = 8	Females N = 15
Home range size (ha)			
Max.	1,067	1,477	1,387
Min.	234	498	177
x̄ ± SE	579 ± 145	896 ± 137	480 ± 88
Primary range size (ha)			
Max.	771	1,017	649
Min.	234	400	46
x̄ ± SE	412 ± 98	596 ± 72	299 ± 50
Home range length (km)			
Max.	5.2	8.2	8.2
Min.	2.7	4.0	1.5
x̄ ± SE	4.0 ± 0.5	5.5 ± 0.5	3.7 ± 0.5
Primary range length (km)			
Max.	4.5	5.8	4.0
Min.	2.7	2.9	1.3
x̄ ± SE	3.7 ± 0.3	4.2 ± 0.3	2.9 ± 0.3

and females were significant for both home range and primary range ($t = 2.90$, $df = 21$, $P < 0.05$; $t = 3.73$, $df = 21$, $P < 0.05$, respectively). Primary range typically included between 84 and 100% of the locations recorded for an individual bird. In terms of area, the primary range accounted for approximately 70% of the cumulative home range in paired males, 76% in unpaired males, and 67% in females.

Maximum length of the home range was positively correlated with home range size ($r = 0.89$, $P < 0.05$), and maximum length of the primary range was correlated with primary range size ($r = 0.66$, $P < 0.05$). As with home range and primary range size estimates, the mean maximum lengths for both home range and primary range were larger for paired males than for either unpaired males or females (Table 1).

As an additional measure of mobility, frequency distributions based on the length of activity radii from the geometric center of activity were calculated for each individual (Hayne 1949, Tester and Siniff 1965). Such a procedure allows additional comparison of mobility without the biases associated with area determinations. Means and standard errors for unpaired males, paired males, and females were 1.03 ± 0.21 km, 1.13 ± 0.19 km, and 0.81 ± 0.11 km, respectively. Although the differences between these mean activity radii are not significant (t-test, $P < 0.05$), the observed pattern is consistent with that recorded for both home range and primary range. When the activity radii for all individuals are combined the resultant distribution has a mean activity radius of 0.90 km, with approximately 58% of all recorded locations falling within a 0.81-km radius of the geometric center of activity.

Home range stability.—Following the method of Gilmer (1971) I checked for the possibility that individuals may tend to limit their movements during the breeding period. By calculating both the minimum area home range and the cumulative increase in home range size for every 7-day interval, a graph similar to the "observation area" curve of Odum and Keunzler (1955) could be constructed for each individual (Fig. 1).

Graphs for individuals fell into one of three categories: (1) continuous increase in cumulative home range—no stability, (2) step-like increases in cumulative home range—temporary stability, and (3) unchanging cumulative home range size over

TABLE 2

COMPARISON OF HOME RANGE STABILITY IN UNPAIRED MALE, PAIRED MALE, AND FEMALE PINTAILS

		No. of individuals showing		
	N	Stability	Temp. stability	No stability
Unpaired males	5	0	1	4
Paired males	8	2	4	2
Females	15	7	6	2

prolonged periods—stability. On this basis 29% of the Pintails demonstrated no stability, 39% demonstrated temporary stability, and 32% demonstrated stability.

Stabilization of the cumulative home range occurred more frequently among females than among either paired males or unpaired males (Table 2). As will be discussed below, reduced mobility during laying and incubation accounts for this trend in females. Among paired males, temporary stability, if achieved, usually occurred during the laying period and/or the postbreeding flocking period following pair-bond dissolution. It is interesting to note that both the paired males that demonstrated prolonged stability were paired to females that made several nesting attempts. The only unpaired male that demonstrated any stability remained on the study area much longer than the other unpaired males. Most of his activity was restricted to a complex of seasonal wetlands frequented by other Pintails.

The recorded "period" minimum area ranges were highly variable and indicated that during any 7-day interval individuals utilized only a portion of their cumulative home range. This pattern was consistent for all individuals regardless of sex and breeding status.

Mobility of nesting hens.—Documentation of changes in female mobility in relation to nesting chronology was complicated by several factors: (1) not all females were captured at the same stage of the breeding cycle; and (2) many nests were lost as a result of predation. To test for differences in prenesting and nesting mobility, minimum area ranges were calculated for each period on the basis of nest chronology. Prenesting ranges included all fix locations from the time of capture until the initiation of laying, and nesting ranges included all locations from the initiation of laying until hatching or nest destruction. Laying periods for individual females included more than one nest in three cases, and observed incubation times ranged from 6 to 23 days. Nine females with known nesting chronologies were tracked for periods long enough to enable calculation of either one or both period ranges.

Female mobility tended definitely to decrease once nesting began. Means and standard errors for the prenesting and nesting ranges were 605 ± 197 ha and 124 ± 25 ha, respectively. The difference between the means is significant ($t = 3.06$, $df = 11$, $P < 0.05$). Maximum lengths of the prenesting ($\bar{x} = 4.2$ km) and nesting ($\bar{x} = 1.8$ km) ranges also differed significantly ($t = 3.47$, $df = 11$, $P < 0.05$). Only one female (# 5515) demonstrated a slight increase in home range size during the nesting period. I believe that this was because her first documented nest was actually a renest. This seems likely because (1) her mobility during the recorded "prenesting" interval was comparable to that of other renesting females, and (2) she was observed giving Repulsion calls and postures (Lorenz 1953, Smith 1968), indicating previous laying and/or incubation soon after capture.

Female mobility appeared to be even further reduced during incubation. Differences between laying and incubation ranges were not tested because of the consider-

able variation in the duration of observed incubation times as a result of predation. However reduced mobility during the incubation period would be expected, as females leave the nest only a few times a day to feed, drink, and bathe.

Five females that initiated several nests showed reduced mobility throughout the nesting and renesting periods, although two of these females made shifts in the primary wetlands being utilized. Available data concerning the distances between successive nests for several *Anas* species (Sowls 1955, Gates 1962, Stotts and Davis 1960, Coulter and Miller 1968) likewise suggest that reduced mobility during the renesting interval is common. Several females that left the study area immediately after nest destruction may have moved to new areas before renesting. Such movements have previously been suggested by Coulter and Miller (1968) and Stoudt (1969) for other *Anas* species.

Mobility of paired males during laying and incubation.—Paired males are more mobile than their mates during the laying and incubation period. Home ranges of five males during this period averaged 316 ha (range 132 ha to 591 ha). Male # 0631 had the smallest recorded nesting home range, but as this male was marked only with a nasal-saddle his mobility was certainly underestimated. Frequent checks of the usual feeding and loafing spots used by the pair indicated that he was often absent when his mate was known to be on the nest. My observations indicate that the mobility of paired males is at its minimum during the first few days of laying, but as the female spends more and more time on the nest as laying nears completion, site attachment by the male rapidly wanes, and male mobility and sociability increase.

Home range and mobility of pairs.—During this study, home ranges were obtained for 11 Pintail pairs. In instances where both members of the pair were radio-marked, home range was calculated on the basis of locations recorded when the pair was together. In cases where only one member of the pair was radio-marked and the other member of the pair was either nasal-saddled or unmarked, home range was calculated solely on the basis of visual sightings.

Recorded pair ranges varied considerably with much of this variation directly attributable to female reproductive chronology. Pair ranges that included both prenesting and nesting periods averaged 509 ± 73 ha (n = 7), while pair ranges that included only the nesting period averaged 167 ± 36 ha (n = 4). Pair ranges in the latter category closely approximate the nesting ranges calculated for nesting hens as would be expected.

Female # 5527, originally marked in 1971 as a laying female, returned to occupy essentially the same areas in both 1972 and 1973. During the spring of 1973, the prenesting movements of this female and her unmarked mate encompassed an area of about 607 ha. Following nesting, the pair was observed on only four different wetlands and associated upland sites in an area of about 122 ha. Reduced mobility was also apparent in the unmarked incubating hen paired to male # 5566. No pair range was calculated in this case as the birds were observed together on only two wetlands, though the male used others when not accompanied by the female.

The home ranges of both individual males and females exceeded the calculated pair ranges in nearly all cases. Much of this is attributable to the greater mobility of males throughout the nesting period and to the movements of females outside the pair range following pair-bond dissolution.

Number of utilized wetlands.—Pintail populations fluctuate dramatically with spring water conditions. Low water levels and drought conditions appear to cause emigration (Smith 1970) or nonbreeding (Leitch 1964), whereas high water levels and

concomitant flooding result in pioneering and high population levels (Hochbaum and Bossenmaier 1972). Because Pintails forage primarily in the bottom sediments of shallow wetlands that are subject to seasonal flooding and drying, such population fluctuations are probably related directly to increases or decreases in shallow wetland habitat (Krapu 1974a). In wet years this foraging habitat is greatly increased not only by the flooding of temporary and seasonal basins, but also by the reflooding of the shallow marsh zones of semipermanent and permanent wetlands. This would appear to explain observed correlations between spring Pintail populations and seasonal wetlands, semipermanent wetlands, and total wetlands as found by Stewart and Kantrud (1974).

All of the individuals used in this analysis utilized water areas of several different classes. The number of wetlands used by individual birds varied considerably, averaging 13 and ranging from 3 to 27. Paired males, unpaired males, and females utilized averages of 17, 12, and 11 ponds, respectively. The number of wetlands used by females reflected primarily reproductive chronology, with more wetlands being used during the prelaying period than during the nesting period. Females of known breeding chronology used an average of 10 different wetlands during the prenesting period and 5 wetlands during the nesting period. The difference between the means is significant ($t = 3.29$, $df = 11$, $P < 0.05$). While laying females often used water areas not utilized previously, this was observed only twice for incubating females. No incubating female was known to frequent more than four different wetlands, and the choice of particular wetlands during this period often appeared to be influenced by male sexual harassment.

DISCUSSION

Throughout the preceding sections I have emphasized the variability in individual home range estimates. Although factors such as wetland distribution and quality, population density, and social interactions undoubtedly affect individual and pair mobility, much of the observed variation can be related to sex, breeding status, and stage of the breeding cycle.

Unpaired male Pintails demonstrated great variation in mobility. Only two of five marked individuals remained on the study area for more than 21 days, and only one male showed long-term localization of activities. All of these males were observed associating with other males and pairs, and engaging in courtship activities. Similar behavior has been reported for unpaired male Northern Shovelers (*Anas clypeata*) (Poston 1974; Seymour 1974a, 1974b), Blue-winged Teal (*Anas discors*) (Drewien 1968), and Gadwalls (*Anas strepera*) (Dwyer 1974).

For both paired males and females, the early season prenesting period was characterized by high mobility and short-term use of many wetlands. As for any specific individual many of these movements were certainly missed, I generally consider individual and pair home range estimates to be rather conservative. Despite this bias, home range estimates calculated for this stage of breeding were consistently larger than those calculated for the nesting period.

In general the mobility of paired males and females decreases through the prenesting period as movements become more localized. While female mobility becomes even further reduced during laying and incubation, male mobility tends to increase during the latter part of the laying period. This difference between males and females is reflected in the tendency for female home range size to stabilize once nesting begins, whereas male home ranges normally exhibited only temporary stabilization.

This pattern of decreasing mobility has been documented in many *Anas* species (Dzubin 1955, Sowls 1955, Drewien 1968, Titman 1971, Poston 1974, Seymour 1974b, Dwyer 1974, Gilmer et al. 1975), but major interspecific differences exist in the degree of activity localization and in the degree and duration of male site attachment (McKinney 1965, 1973). When compared to other species studied thus far, it is apparent that Pintail pairs are much more mobile during the laying and incubation periods, and that site attachment in male Pintails is normally reduced and brief. The lack of strong site attachment, the frequent erratic movements and the pronounced sociability that characterize male Pintails have previously been noted by Dzubin (1955, 1969), McKinney (1965, 1973), and Smith (1968). Male mobility was undoubtedly greater than female mobility at all stages of the breeding cycle, as males frequently left their mates to associate with other males and pairs and to court and/or chase "strange" females.

Working in the pothole region of South Dakota, Drewien (1967, 1968) found the home ranges of a Pintail pair and a Pintail female to be approximately 486 ha and 283 ha, respectively. Although the reproductive chronologies of these birds were unknown, the home range estimate for the pair probably included the prenesting and nesting periods as the pair was followed for about 6 weeks. These estimates are quite similar to the home range estimates obtained in this study.

Although home range information has been gathered for relatively few *Anas* species to date, species-specific mobility patterns are already becoming apparent. Recorded pair home range estimates for Cinnamon Teal (*A. cyanoptera*), Blue-winged Teal, Shovelers, and Gadwalls have generally been less than 130 ha (Gates 1962; Drewien 1967, 1968; Evans and Black 1956; Dzubin 1955; Sowls 1955; Poston 1974; Seymour 1974b). Pair home range estimates for the Mallard (*A. platyrhynchos*) range from 200 to 283 ha (Dzubin 1955, Drewien 1968, Gilmer et al. 1975), and a single pair of Green-winged Teal (*A. crecca*) was found to have a home range of approximately 243 ha (Drewien 1967). In comparison with these species, the breeding home range of a pair of Pintails is quite large.

Such comparative differences between species are also consistent for other measures of mobility such as maximum home range length and mean activity radius. Previously reported home range lengths vary from 1.0 km for Blue-winged Teal (Dzubin 1955) to 2.6 km for Mallards (Gilmer et al. 1975); while reported mean activity radii range from 0.29 km for Blue-winged Teal (Evans and Black 1956) to 0.58 km for Mallards (Gilmer 1971). As with home range size, estimates of these parameters are comparatively greater for Pintails than the other species studied thus far.

Mobility, as reflected by breeding home range size, is an important component of a species social system, and is related to many other aspects of social behavior. As McKinney (1973, 1975) pointed out, species with low mobility tend to be more territorial and demonstrate pronounced male-male hostility, distant threat displays, long-lasting pair-bonds, well developed three-bird chases and a low frequency of promiscuous copulations. Conversely more mobile species like the Pintail are less territorial and correspondingly male-male hostility is reduced, pair bonds are weaker, aerial pursuit behavior is more variable, and promiscuous copulations are more frequent.

While many factors have certainly been involved in the evolution of specific *Anas* social systems (cf. McKinney 1973), several lines of evidence suggest that much of the observed diversity may be related to the spatial and temporal aspects of available

food resources and whether or not these resources are "economically defensible" (Brown 1964, Brown and Orians 1970). It is now apparent that egg-laying is energetically demanding for ducks (King 1973) and large amounts of protein in the form of aquatic invertebrates are required (Holm and Scott 1954; Krapu 1972, 1974a, 1974b; Swanson and Meyer 1974; Swanson et al. 1974). These energetic and dietary demands are reflected in dietary shifts during the prelaying, laying, and postlaying periods (Krapu 1972) as well as in increased feeding rates during the laying period (Bengston 1972, Dwyer 1974, Swanson et al. 1974). As a result, both McKinney (1973, 1975) and Dwyer (1974) have postulated that in territorial species such as the Shoveler and the Gadwall chasing serves to secure a food supply and to provide undisturbed feeding time for the female.

Although Young (1970) has demonstrated a relationship between resource levels and exclusive feeding areas for the Common Sheld-Duck (*Tadorna tadorna*), no equivalent studies have been carried out thus far for any *Anas* species, but research to date indicates that: (1) different *Anas* species are utilizing different food resources even when occupying the same wetland habitat (Krapu 1972, Swanson et al. 1974); (2) individuals often respond quickly to shifts in food availability in space and time; and (3) specific invertebrate populations fluctuate seasonally within and between wetlands (Swanson et al. 1974). Additional research on resource patchiness is clearly warranted, and may provide a better understanding of the specific differences in mobility and social behavior within the genus *Anas*.

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