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The **American Ornithologists' Union** will hold its **96th Stated Meeting** during the week of 14–18 August 1978 at the University of Wisconsin-Madison at the invitation of the Department of Wildlife Ecology and the Department of Zoology of the University of Wisconsin-Madison, the Wisconsin Society for Ornithology, and the Madison Audubon Society. A Circular of Information providing details of the meeting and a formal call for papers will be sent to the A.O.U. membership. Chairman of the Local Committee is Dr. Stanley A. Temple, Department of Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53706. Chairman of the Committee on Scientific Program is Dr. Ralph W. Schreiber, Natural History Museum, 900 Exposition Boulevard, Los Angeles, California 90007.

THE TIMING OF EGG LAYING BY NORTHERN GEESE

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ABSTRACT.—The delay between the peak arrival and peak of nest initiation by Cackling Geese (*Branta canadensis minima*) in an unusually early spring season coincided with the time required for rapid yolk development. Even though nesting habitat was available, Cackling Geese could not nest earlier than they did because of their physiological state. A review of available data reveals that Canada Geese and Brant (*Branta bernicla*) regularly nest 10–13 days after their peak arrival at nesting areas, or after their departure from final spring staging areas. This is the interval required for rapid yolk development. Lesser Snow Geese (*Anser caerulescens caerulescens*) and Ross' Geese (*Anser rossii*) commonly nest within 3–5 days of their peak arrival at nesting areas. It is suggested that the stimuli causing rapid yolk formation are related to the events just prior to, or at the time of, migration from the usual final spring staging area to nesting areas for Brant and Canada Geese, and at the time of the migration to final staging areas by Lesser Snow and Ross' Geese. This plasticity in ovary preparation is related to weather patterns that affect spring thaw and the availability of nest sites. The probable ecological advantages of the varying patterns of ova formation in different species and populations of geese are related to the premium placed on earliest possible nesting versus maximizing reproductive opportunity by ova formation after arrival at the nesting area. *Received 23 September 1976, accepted 20 September 1977.*

GEESE breeding in northern latitudes commonly migrate to their nesting locations before snow and ice melt is completed. Egg laying is reported to be controlled by the availability of nest sites as functions of the disappearance of snow and ice, presence of open water around a nest site, recession of flooding caused by the melt, and the cessation of wind storms (Cooch 1958, 1961; Barry 1962, 1967; MacInnes 1962; Ryder 1967; Mickelson 1975). Annual arrival of geese on nesting grounds is often more predictable than the phenology of the spring thaw (Cooch 1961, Barry 1962). It is generally considered that geese are capable of egg laying almost immediately after their arrival on the nesting grounds, implying that the control of rapid ovarian follicular development is related to stimuli operative several days prior to the final migration to the nesting grounds. The purposes of this paper are: (a) to present data on the nesting chronology of Cackling Geese (*Branta canadensis minima*) that suggest a different timing of rapid yolk formation, at least for this subspecies; and (b) to review data on several species and populations that suggest variation in the timing of mechanisms influencing nesting chronology, and their probable adaptive significance to different populations.

METHODS AND STUDY AREA

I studied the nesting ecology of Cackling Geese between 3 May and 1 July 1974 on the Yukon-Kuskokwim River Delta, Alaska (61°23′N, 165°27′W) in the vicinity of the U.S. Fish and Wildlife Service field station at Old Chevak, Clarence Rhode National Wildlife Range. Four study plots were established from 0.8 to 8.9 km (0.5 to 5.5 mi) north of the site described by Mickelson (1975). The study plots incorporated two basic elevations and habitat types containing ponds used by nesting geese (Mickelson 1975). Lowland flood plains were about 0.5 m above mean high tide and were characterized by sedges (*Carex rariflora* and *C. mackenziei*) and speargrass (*Poa eminens*). Upland tundra was about 1.2 m above mean high tide and was characterized by *Sphagnum* spp., tea (*Ledum* spp.), crowberry (*Empetrum nigrum*), dwarf birch (*Betula nana*), and oval leafed willow (*Salix ovalifolia*).

Dates of nest initiation (first egg of a clutch) were determined from finding nests before clutches were

TABLE 1. Chronology of events related to Cackling Goose nesting

Event	1969[a]	1970[a]	1971[a]	1972[a]	1974
Arrival of investigator	12 May	4 May	16 May	8 May	3 May
Meltwater flooding	13 May	18 May	28 May	26 May	3 May
Ice gone from ponds[b]	25 May	27 May	5 June	13 June	19 May
First Cackler seen	12 May	9 May	16 May	9 May	4 May
Peak arrival of Cacklers	?	?	23–25 May	23–26 May	12–13 May
First nest initiated	20 May	21 May	1 June	30 May	19 May
Peak of nest initiation	23–24 May	28–29 May	6–7 June	2–5 June	24–25 May
80% (+) of nests initiated by:	29 May	1 June	9 June	6 June	30 May
Interval between peak arrival and peak nest initiation	—	—	13 days	10 days	12 days
Average clutch size[c]	4.61	4.57	4.52	4.97	4.82

[a] From Mickelson (1973, 1975)
[b] See text
[c] From nests being incubated in Mickelson's study

complete and by back-dating from the day of hatching by allowing 26 days for incubation and a laying rate of 1 egg per day (Mickelson 1975). Geese were collected throughout the spring to obtain data on physical condition and gonad development. Unincubated eggs from nests at which females were collected were saved for studies on yolk development by C. R. Grau (cf. 1976) and T. Roudybush.

RESULTS AND DISCUSSION

SPRING THAW

Spring thaw in 1974 was exceptionally early. C. J. Lensink, former manager of Clarence Rhode, considered it the earliest ice breakup in the 13 years of his experience in the area (pers. comm.). Winter snow cover was unusually light and was 90–95% gone as judged from aerial photographs taken on 3 May. Nearest weather stations were on the Bering Sea coast 38.6 km (24 mi) from the study area, but these data may not precisely reflect snow and ice conditions of the inland study areas.

Evidence of the early spring was best indicated by the lowland flood plains, which were covered with meltwater when we arrived on 3 May. This flooding was 10–25 days earlier than during Mickelson's (1973, 1975) 4-year study (Table 1). Because of the shallow snow cover and negligible precipitation in May, meltwater was less than normal and drained rapidly off the lowlands. Ponds used for nesting by geese became ice-free between 13 and 19 May.

Larger, deeper ponds in the upland tundra with few or no islands were 90% ice-free by 23 May, although a few contained some ice until 28 May. These dates should not be compared directly to Mickelson's records because his study area was predominantly lowland containing shallower ponds which become ice-free sooner than larger, upland tundra ponds.

MIGRATION AND NESTING CHRONOLOGY

Numbers of Cacklers seen daily varied from 4 on 4 May to 37 on 10 May. On the morning of 13 May, flocks of 20± were common and there were hundreds of Cacklers in the vicinity. This peak arrival was 12 days earlier than in the retarded springs of 1971 and 1972 (Mickelson 1973, 1975) (Table 1), but was probably little different than in the "average" or early years of 1969 and 1970 for which Mickelson only reported that numbers of geese peaked in mid-May.

As usual for arctic geese, nesting in 1974 was highly synchronized and 89% of all Cackler nests were initiated within 10 days (22 May–1 June). Greater synchrony

TABLE 2. Ovarian follicle development of adult female Cackling Geese collected before egg laying

Date	Largest ovarian follicle diameter (mm)	Projected date of possible nest initiation[a]
10 May	9	20 May
13 May	20[b]	19 May
14 May	9	24 May
15 May	23	20 May
18 May	23	23 May
19 May	8	29 May
30 May	First egg in oviduct	30 May

[a] Based on estimated growth rate of 3 mm per day and an average diameter of 39 mm at ovulation—see text
[b] Ruptured by shot—size estimated

occurs in late seasons than in early ones (Mickelson 1973, 1975). An abundance of suitable ponds and nest sites free from snow, ice, or meltwater were available for 6–9 days before the peak of nest initiation by Cackling Geese. Of prime importance was the fact that the time interval between peak arrival of migrants and peak nest initiation was 10–13 days regardless if the season was exceptionally early, as in 1974, or late, as in 1971 and 1972 (Table 1).

EGG DEVELOPMENT

Seven adult females were collected before they had laid eggs (Table 2). None had obvious atretic follicles. The average diameter of the yolk of 19 eggs measured by Roudybush (pers. comm.) was 39 mm. When rapid ovarian follicular development begins in domestic fowl it culminates only in ovulation or atresia and not in arrested development, and the rate of yolk growth is essentially linear after the first day or two (see review by Gilbert 1971). If this process is the same in geese, then the earliest possible date of potential egg laying of the collected birds can be estimated by comparing the size of the largest follicle to the average size at ovulation (Table 2). None of the females collected could have laid eggs before 19 May.

Grau (cf. 1976) determined that it took 12–13 days for the yolk of seven Cackling Goose eggs and three *B. c. moffitti* eggs to develop (pers. comm.). The delay between peak arrival and peak nest initiation (Table 1) corresponded almost exactly to the time necessary for rapid yolk development. Nesting by most of the population could not have been initiated earlier than recorded in 1974 even though habitat was available.

The pattern of spring migration by Cackling Geese between their time of departure from California in early- to mid-April and arrival on the nesting grounds is not well known. It appears that the stimulus for rapid ovarian follicular development occurred at the same time as the initiation of the final migration flight into nesting areas, or perhaps coincided with arrival itself.

OTHER CANADA GOOSE STUDIES

Low Arctic Tundra.—Dates of peak arrival and the mid-point of nest initiation (which closely approximates the peak of nest initiation) for small Canada Geese (*B. c. hutchinsii-parvipes* complex of MacInnes 1966) at the McConnell River Delta, Northwest Territories, Canada (60°50'N, 94°W) reported by MacInnes (1962) and MacInnes et al. (1974) are presented in Table 3. Disappearance of 50% of the snow cover was used as an index of weather and nest site availability, although the rate of snow melt may be highly variable in relation to pond availability.

TABLE 3. Chronology of events related to nesting of small Canada Geese at the McConnell River Delta, Northwest Territories (from MacInnes 1962 and MacInnes et al. 1974)

	Snow 50% gone	Peak arrival	Mid-point of nest initiation	Interval (days) between peak arrival and peak nest initiation
Early springs				
1960	28 May	29–30 May	8 June	9–10
1965	2 June	31 May	10 June	10
1966	1 June	30 May	8 June	9
1968	8 June	31 May	12 June	12
1971	22 May	28 May	6 June	9
Average	31 May	28 May	9 June	10
Late springs				
1959	11 June[a]	5 June	14 June	9
1964	5 June	4 June	12 June	8
1967	1 June	5 June	10 June	5
1969	12 June	7 June	17 June	10
1970	1 June	5 June	12 June	7
Average	6 June	5 June	13 June	8

[a] From MacInnes (1962); reported as both 4 and 9 June in MacInnes et al. (1974)

Major arrival of migrants was "early" in 5 years (28–31 May) and the delay to peak nest initiation was 9–12 days ($\bar{x} = 9.9$). These results suggest that the delay might have been necessary for the maturation of ovarian follicles that were stimulated by the same factors (or at the same time) that stimulated the final migration to the nesting area. The timing of arrival to, and location of, the final spring staging areas after these geese leave the prairies of the Dakotas and southern Manitoba in early- to mid-May are not well documented.

Major arrival of migrants was late in 5 years (4–7 June) (Table 3), and the delay to peak nesting varied from 5–10 days ($\bar{x} = 7.8$). Since there is probably little variation among races of Canada Geese in the time required for rapid ova formation, follicular development was proceeding in at least three of these years before the birds arrived on the nesting area, with the result that nest initiation was not delayed as much as arrival with respect to early seasons. This suggests that rapid follicular growth was stimulated at essentially the same time as in early seasons, but that the final migration was interrupted or prevented by unfavorable conditions. Presumably, weather conditions changed soon enough for the geese to arrive and begin egg laying with little delay compared to early seasons.

In the other two late seasons, the delay to peak nesting was 9 or 10 days, as in early seasons. If ovarian follicular development was proceeding as in other late seasons, nesting was prohibited by lack of suitable nest sites. These 2 years (1959 and 1969), as indexed by snow cover, were by far the two latest spring thaws, and follicular atresia and reduced clutch size should have resulted. Data presented for 1959 (MacInnes 1962) are inadequate to judge this, but, indeed, in 1969 the modal clutch changed from the usual 5, and occasional 4, to 3 eggs (MacInnes et al. 1974). There was also a shift to 3-egg clutches in 1967 (a late season of arrival, but short delay between arrival and egg laying, Table 3). Nutritional state affects the timing and number of eggs laid (cf. Jones and Ward 1976). Possibly geese were in poorer condition upon arrival based on food during migration, as suggested by MacInnes et al. (1974), but this could also be related to delay by interrupted migration once rapid oocyte formation was triggered and atresia resulting after development had proceeded for 12–13

TABLE 4. Chronology of events related to nesting of *B. c. interior* at Kinoje Lake, Ontario

Event	1967	1968	1969
Arrival of investigators	7 April	7 April	7 April
First geese seen	12 April	10 April	13 April
Majority of Bog-ponds ice-free	16 May	18 April	5–6 May
First major goose departure from Horicon, Wisconsin[a]	20–21 April	16–17 April	19–20 April
First major arrival of geese	28 April	16–17 April	24 April
First nest initiated	3 May	19 April	23 April
Peak of nest initiation (mid-point)[b]	14–15 May	27–28 April	1–2 May
Interval between peak arrival and peak nest initiation	16–17 days	11–12 days	7–8 days
Interval between first major departure from Wisconsin and peak nest initiation	24–25 days	11–12 days	11–13 days

[a] From R. A. Hunt (pers. comm.)

[b] Based on data from 81 and 112 dateable nests in 1968 and 1969, respectively; estimated for 1967 from 40 nests

days (thus resulting in poorer condition upon arrival, irrespective of their condition earlier in the spring).

Sub-Arctic Muskeg.—Observations of migration, nest site availability, and nest initiation for Canada Geese (*B. c. interior*) at Kinoje Lake, Ontario (51°35′N, 81°45′W) are provided in Table 4. Results are from a Mississippi Flyway Council and Ontario Ministry of Lands and Forests study by Raveling and H. G. Lumsden (unpublished data). Habitat descriptions may be found in Hanson and Smith (1950).

Availability of suitable nest sites was accurately indicated by the dates of ice disappearance from bog-ponds because flooding did not occur in the raised peat bogs. Spring thaw was unusually early in 1968 and nesting habitat was available when the geese arrived. Peak of nest initiation, however, did not occur until 11–12 days after the departure of the first major numbers of geese from the spring staging area and their apparent nonstop flight to the nesting areas. This suggests that rapid oocyte formation began just before or at the time of initiation of this migration and the temporal delay to nest initiation was necessary for ova maturation.

The migration flight of the first major departure of geese from Wisconsin in 1969 was apparently interrupted as major arrival did not occur until 4–5 days later (when weather at Kinoje changed and warming south winds occurred). In this case, as noted above for some years at the McConnell River (Table 3), the 7–8 day delay between peak arrival and peak nesting indicates that rapid yolk formation was proceeding when the geese arrived. The time interval between their departure from Wisconsin and peak nesting suggests again that rapid follicular growth was stimulated just before or at the same time as was the last migration flight.

The spring of 1967 was exceptionally retarded (latest in 17 years) as indicated by late migration, ice breakup, and nesting in Table 4. Follicular atresia should have resulted. Clutch size in 1967 (4.37) was significantly smaller than in 1968 (4.95) and in 1969 (4.64). There was not a significant difference between clutch sizes for 1968 and 1969. Raveling and Lumsden (unpublished) concluded that in addition to reduced production because of decreased size of clutches, large numbers of geese did not nest in 1967.

OTHER SPECIES

Brant.—The best data on the relationship of gonadal development to nesting chronology were provided by Barry (1962) for Atlantic Brant (*Branta bernicla hrota*) nesting on Southampton Island, Northwest Territories. Brant arrived on 7 or 8 June regardless of the progress of the spring thaw. In 1953, nesting habitat was available at the time of Brant arrival, but the peak of egg laying was 10 days later. This pattern of regular arrival and at least a 10-day delay to peak nest initiation, regardless of season phenology, was also evident in Pacific Brant (*B. b. nigricans*) (Barry 1967). This, again, suggests that rapid ovarian follicular growth was stimulated just prior to or at the same time as final migration to, or arrival at, nesting areas. Egg laying probably could not have occurred earlier because of the time needed for ova maturation. When nesting was delayed longer than 10–13 days, clutch sizes decreased because of follicular atresia (Barry 1962).

Lesser Snow Goose.—Cooch (1958:52) reported that egg laying by Lesser Snow Geese (*Anser caerulescens caerulescens*) usually began within 3 days of their arrival at Southampton Island in Hudson's Bay. Barry (1967) collected adult female Lesser Snow Geese with mature ovarian follicles on 31 May and 3 June, in a year (1960) when peak arrival was 1 June at the Anderson River Delta, Northwest Territories (69°44′N, 128°44′W). At this location, the final flight to nesting sites was about 322 km (200 mi) from their final staging area on the MacKenzie River in the interior where spring thaw was much earlier than at coastal nesting areas. Geese arrived at this staging area in mid-May, but exact dates of peak arrival were not reported or known. It appears that the time at which rapid ova maturation begins in Lesser Snow Geese coincides with their migration to, or arrival at, the final staging area before flight to the nesting areas. When nesting is delayed longer than 3 days, clutch sizes decrease (Cooch 1961).

Ross' Goose.—It is clear from Ryder's (1967, 1972) data on Ross' Geese (*Anser rossii*) in the Perry River region of the Northwest Territories (67°22′N, 102°10′W) that they are similar to Lesser Snow Geese in being capable of nesting soon after arrival at nesting areas. The chronology and pattern of Ross' Goose migration between the prairies of east-central Alberta and their nesting areas are not well known. Arrival dates were more variable than intervals between arrival and nesting. Thus, factors which stimulated migration to the nesting areas were closely related to weather conditions resulting in thaw at the nesting areas and availability of nest sites. Correlated with this predictability of available nest sites was stimulation of rapid ovarian follicle growth sufficiently in advance of the birds' arrival so that egg laying proceeded within at least 3 days, for the bulk of the population. Massive failures of Ross' Goose reproduction during Ryder's studies did not occur as they have in Lesser Snow Geese (Cooch 1961), but neither were the delays from peak arrival to peak of nesting as long as in some years for Lesser Snow Geese.

NATURE OF STIMULUS FOR OVA MATURATION

Photoperiod stimulation is responsible for testicular recrudescence in most temperate and high latitude zone birds (see reviews by Lofts and Murton 1968, 1973; Farner and Lewis 1971; Lofts 1975). Females also respond to photostimulation, but in the few species studied to date a block to ovarian growth occurs at the onset of rapid yolk development if appropriate proximate factors are lacking (usually mate and appropriate nest site). Whether or not the oocytes develop under photostimulation alone, ovulation can be inhibited by the lack of appropriate nesting conditions, and this has been demonstrated in both captive and wild geese (Wood 1964, Barry 1962).

It is conceivable that rapid yolk synthesis is irreversibly controlled by photoperiod at a precise time in geese and that different timing response mechanisms (see Murton and Kear 1973) in different species account for the variation in time of development reviewed here. It is most likely, however, that geese require additional proximate stimuli to cause rapid oocyte development as for other wild species studied to date (Lofts and Murton 1973). Geese in captivity at temperate latitudes, including species that normally spend the winter near the latitudes at which they were captive, commonly nest up to a month earlier than in the wild without having to experience a transition to arctic daylength (Davies, et al. 1969, Murton and Kear 1973). If photoperiod caused full follicular development this early in the wild, then atretic follicles should be apparent upon the arrival of geese at nesting areas. Only the follicles corresponding to a normal clutch (4–7) develop rapidly in sequence (Wood 1964). In four adult female Cackling Geese collected at the onset of incubation in the 1974 season, the number of atretic follicles plus clutch size equaled the normal full clutch potential, as also reported for Brant and Lesser Snow Geese by Barry (1962, 1967).

For Canada Geese and Brant, stimulation of ova formation was associated with the events immediately preceding, or at the same time of, final migration to nesting areas. In early seasons, ova maturation in Canada Geese occurred mostly after arrival on nesting grounds. Arrival of Canada Geese on nesting areas was more variable than in Brant and, at least in some seasons, much ova development occurred before arrival at nesting sites. The Kinoje Lake data suggest that the stimulation for rapid ova development was, however, still associated with their migration departure from the usual final spring staging area. Since Lesser Snow and Ross' Geese regularly nest within 3–5 days of their major arrival, data on arrival at their final staging areas from which they proceed to nesting grounds are needed. Barry's (1967) observations suggest that rapid oocyte formation is stimulated at the time of arrival to the migration staging area closest to the nesting grounds.

Variability in the exact timing of ova maturation coupled with weather patterns that result in thaw and the availability of nest sites would be the most precise adaptation for successful reproduction in geese (for females). Spring migrations are variable in most species in the exact time of occurrence in association with weather, especially changes in frontal systems which result in warming southerly winds (cf. Blokpoel and Gauthier 1975). Following winds presumably reduce the energetic costs of migrating, but the same weather patterns will usually hasten spring thaw. Thus, arrival on or in proximity to nesting areas in synchrony with slight yearly variations in seasonal phenology is assisted. Synchronization of ovary preparation for laying with these same weather patterns would allow the best chance for maximum reproductive success. I suggest that the gonadotropin release responsible for final ova maturation (see Follett and Davies 1975) is stimulated at the same time as, or just before, this final migration. Perhaps the cues by which the migration is presumably stimulated also trigger this hormonal release.

Increased metabolic activity associated with hormonal release and the onset of this final migration may be related to accelerated ovary development once the animal is photoresponsive. Rutledge (1974) demonstrated that spermatogenesis in the starling (*Sturnus vulgaris*) was characterized by elevated body temperature. Elevated thyroid hormone secretion is also implicated by the increased metabolism and is related to avian migration and Zugunruhe, and to normal gonad development in domestic mallards (*Anas platyrhynchos*) (see Assenmacher 1973 for review). Although large doses of thyroxin can have deleterious effects on egg production in domestic fowl, moderate rates of administration, or naturally high rates of secretion of thyroxin, increase egg production (see Falconer 1971 for review). The fact that activation of the thyroid could be part of the mechanism bringing about testicular regression (Assenmacher 1973) in males at the same time as stimulating rapid yolk formation in females is not contradictory. Barry (1962) demonstrated that Brant testes were regressing in weight while ovary development was proceeding. Thus, it is plausible that stimuli that affect the timing of the final migration flight of geese to or near their nesting grounds also stimulate a complex hypophyseal hormone release affecting thyroid secretion that metabolically affects, or interacts with, gonadotropins or gonadal steroids to cause ova development at the most propitious time for reproduction to occur.

Appropriate pair behavior is also usually necessary for follicle maturation (see review by Lofts and Murton 1973). Copulations by geese occur before arrival on nesting areas and are rarely observed early in spring migration (Cooch 1958, 1961; Barry 1962, 1967; MacInnes 1962; Ryder 1967; Mickelson 1975; personal observations). This aspect of sexual behavior probably peaks at geographic areas from which geese make their final migration to nesting grounds and thus it coincides with the time at which rapid ova formation is initiated. As eggs of geese must usually be fertilized by stored sperm, copulation might normally be necessary to stimulate the hormone release resulting in yolk development.

The importance of pair relations in preparation for reproduction by geese is further indicated by weight changes of individually marked Giant Canada Geese (*B. c. maxima*) of known social status weighed at least twice during the period of spring fat accumulation (R. M. McLandress and Raveling, unpublished data). Weights of seven adults that were paired increased 27 to 38%. Weight declined 7% and gained less than 1% in two unpaired adults.

ECOLOGICAL ADAPTATIONS

The general adaptive nature of early nesting by northern geese is well known. Later nesting than that observed would result in insufficient time for molt and preparation for migration in autumn (Cooch 1961, Barry 1962). Synchrony of hatching with the temporal availability of high-protein new growth of sedges and grasses is required for growth of the young (Murton and Kear 1973). Earlier nesting than that usually observed would expose eggs to freezing, access to mammalian predators because of connection of islands to the mainland by ice, and flooding at the time of spring runoff.

Within the above constraints, different species of geese have different migration patterns in relation to ova maturation and ability to lay eggs upon arrival at nesting areas. Brant nesting habitat is usually the latest available and they arrive later than other geese. This is ecologically, and evolutionarily, related to their sea coast habitat and marine food supply. Their small size, short growth period, and marine habitat, which freezes later in autumn than inland ponds and lakes, allows later nesting than the other species. Ova preparation after arrival rather than before seems to be the best strategy for maximum reproductive opportunity for Brant.

The pattern exhibited by Lesser Snow and Ross' Geese would be best when the earliest possible nesting in all years is at a high premium. Ross' Geese nest on larger lakes to the interior of delta habitat favored by Lesser Snow Geese. These lakes thaw slightly later than pond and delta habitat and Ross' Geese nest later than Lesser Snow Geese. Presumably, their small size and shorter period of growth is permissive to use of this habitat. The premium for earliest possible nesting by Lesser Snows in terms of the time required for hatching, molt, and growth related to the summer season was provided by Cooch (1958, 1961).

It is difficult to reconcile why small Canadas exhibit a different pattern of ova preparation in relation to arrival than Lesser Snow Geese. Perhaps it is a function of the proximity of habitat and food supplies important in the timing of peak spring weight accumulation during migration. It is also possible that Canada Goose reproduction is not as severely constrained by late spring seasons as it is for Lesser Snow Geese. Canada Geese nesting at the same latitudes as Lesser Snow Geese are slightly smaller in body size (except at the two most recent and southern Lesser Snow Goose colonies), and presumably they could reach flight stage in later seasons that would select more strongly against Lesser Snow Geese. Thus, a more variable ova maturation in relation to events permitting arrival and nesting by Canada Geese would be a more effective average response than the more all-or-none strategy exhibited by Lesser Snow Geese.

Almost complete failures of reproduction by Brant and Cackling Geese on the Yukon-Kuskokwim Delta, Alaska, because of late spring weather, have never been recorded (C. J. Lensink, pers. comm.) as they have for Lesser Snow Geese and Brant at higher latitudes in the interior arctic (Cooch 1961, Barry 1962). The maritime influence on the west coast results in earlier thaws and later freezes than on the Arctic Ocean and Hudson's Bay coasts. Ova formation by Cackling Geese (and, again, for Brant) after arrival on nesting areas provides the most flexible response to obtain maximal production in relation to annual variations in availabilty of nesting habitat because seasons are never, or rarely, so retarded as to make nesting ill-adaptive.

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EXPERIMENTAL ANALYSIS OF NEST PREDATION IN AN OLD-FIELD HABITAT

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ABSTRACT.—Experimental nests, each containing two Japanese Quail eggs, were systematically distributed in 10 ha of old-field habitat near Oxford, Ohio, to analyze the effect of human visits, vegetation type, concealment, and normal parental nesting behavior on the likelihood that predators will discover open nests. Each week for 12 weeks, 20 varying nest sites were selected and used. From 4 May to 26 July 1975 we exposed these nests for 6 days apiece in 240 locations. We made daily visits to 10 nests each week, none to the other 10. Seasonal rates of predation of experimental nests followed the pattern observed for natural nests in other old-fields. Daily visits did not affect the likelihood that predators would discover experimental nests. Well concealed experimental nests were no less likely to suffer predation than poorly concealed ones. Type of vegetation chosen for the experimental nest site was not related to predation rate. Comparison of survival of natural and experimental nests revealed no significant differences in numbers succumbing to predators or in the duration of survival of nests preyed upon. These experimental results indicate that visits to nests by investigators do not appear to affect success or failure. *Received 2 June 1976, accepted 10 December 1976.*

THE nest success of most birds that breed in some old-field habitats in the eastern United States is quite low, averaging only about 20%. Here nest success varies seasonally, with low success in May and early June followed by higher success in late June, July, and August. Predation of nest contents causes most losses (Nolan 1963, Ricklefs 1969, Thompson and Nolan 1973).

The great pressure of nest predation on open-nesting altricial birds is generally thought to be responsible for the evolution of their short incubation and nestling periods (Lack 1968: 172; Ricklefs 1969: 41–42; Welty 1975: 329). The demonstrable effect of nest predation on reproductive success and its inferred effect as a selective evolutionary force lead one to ask what factors determine whether a nest will succeed or fail.

The investigator's trips to studied nests could conceivably increase, or even decrease, the likelihood that they would be found by a predator (Stoddard 1931, Earl 1950, Willis 1973, Mayfield 1975, Picozzi 1975), a possibility that must be investigated before the importance of other factors can be evaluated properly. Beyond this possible observer effect, the many suggestions that have been advanced to explain how predators find nests can be grouped into four general categories: (1) Predators are attracted by parental activity (Skutch 1949); (2) predators are attracted by the cries of begging young (Skutch 1949, Young 1963, Perrins 1965); (3) predators respond to olfactory cues emanating from nest, parents, eggs, or young (Henry 1969, Willis 1973, Lill 1974); and (4) predators locate nests visually (Lill 1974). The problem of evaluating these possibilities is complicated by the fact that nest predators include mammals, snakes, and birds, each of which could be using different cues or combinations of cues. To date, most studies investigating cues used by predators have involved ground-nesting birds, particularly waterfowl, gulls, and gallinaceous species, which seem especially vulnerable to mammalian and avian predators (Earl 1950, Hammond and Foreward 1956, Keith 1961, Matschke 1965, Evans and Wolfe

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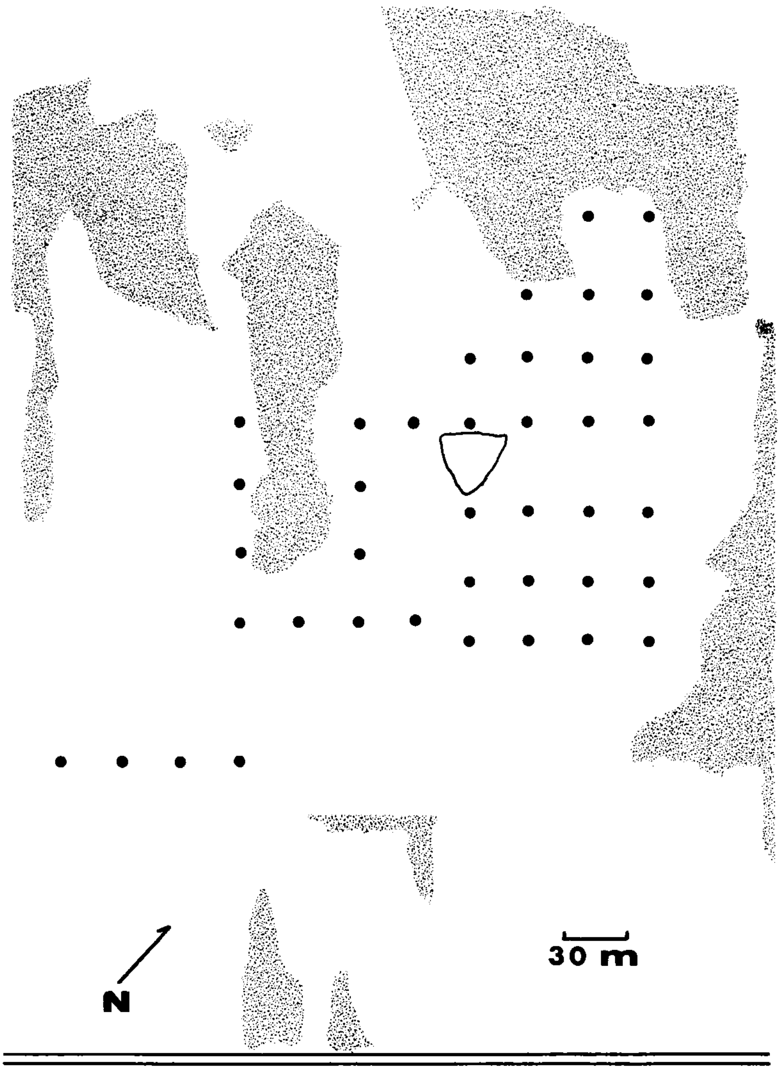

Fig. 1. Bachelor Estate study area and location of points used to determine placement of experimental nests. Shaded areas are woods.

1967, Tinbergen 1968, Henry 1969, Klimstra and Roseberry 1975, and Picozzi 1975). In old-field habitats, where open-nesting birds are exposed to an assortment of nest predators that includes snakes as well as birds and small mammals (Nolan 1963, Thompson and Nolan 1973), little is known about the effects on nest success of either observer activity or the role of the aforementioned cues. The experiment herein reported was designed to investigate some of these questions.

STUDY AREA AND METHODS

We performed the experiment from May through July 1975 at Miami University's field station on the Bachelor Estate approximately 2 km west of Oxford, Butler County, Ohio. The 10-ha tract (Fig. 1) consisted of a group of contiguous upland agricultural fields abandoned for varying lengths of time. Osage orange (*Maclura pomifera*), multiflora rose (*Rubrus* sp.), and red cedar (*Juniperus virginianus*) are among the most common woody species; goldenrod (*Solidago* spp.) and asters (*Aster* spp.) are the dominant forbs.

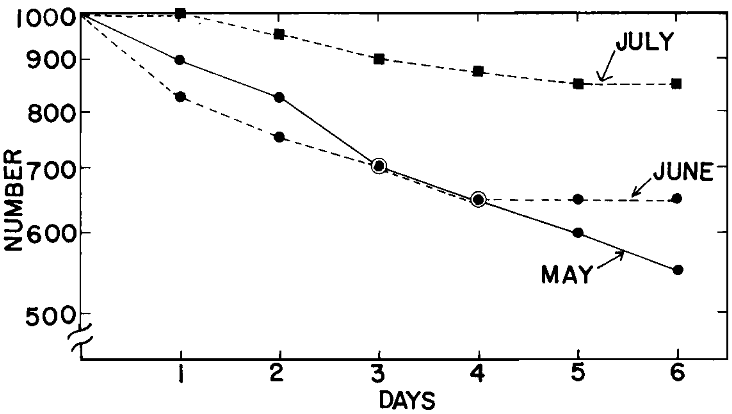

Fig. 2. Survivorship curves of visited experimental nests, according to month, assuming an initial cohort of 1,000 nests.

The most abundant breeding birds are the Cardinal (*Cardinalis cardinalis*), Mourning Dove (*Zenaida macroura*), Field Sparrow (*Spizella pusilla*), Yellow-breasted Chat (*Icteria virens*), Red-winged Blackbird (*Agelaius phoeniceus*), American Goldfinch (*Carduelis tristis*), Song Sparrow (*Melospiza melodia*), and American Robin (*Turdus migratorius*).

We placed abandoned nests of American Robins, Cardinals, and Field Sparrows, each containing eggs of the Japanese Quail (*Coturnix coturnix*), in nest sites typically used by the aforementioned species. Twenty such experimental nests were set out on the Sunday of each of 12 weeks, beginning on 4 May 1975, and from these 20 were selected 10 by lot to visit daily. These 10 we inspected in the late afternoons or early evenings but did not visit the remaining 10 nests until Saturday. On that day, after their 6 days of exposure to predators, we collected and removed from the study area any eggs that remained in the 20 nests. On Sunday we moved all nests to different locations, added fresh quail eggs, and repeated the procedure. Thus during the 12 weeks we placed experimental nests at 240 different locations.

As the nests deteriorated through wear, we replaced them with fresh ones. Quail eggs, which we obtained from a laboratory colony, were either fresh or had been refrigerated for a period not exceeding 6 weeks before being used.

Dispersion of experimental nests within the 10 ha was achieved by first establishing 40 evenly spaced points over the tract (Fig. 1), then using alternate points for placement of each week's 20 nests. Actual locations of nests in relation to each point were determined by selecting two numbers between 0 and 18 from a table of random numbers. These numbers dictated the distance in paces and compass direction from the point (even, north and east; odd, south and west) that each nest was to be placed. We then put the

TABLE 1. The outcome of visited and unvisited experimental nests, according to month

	Preyed upon								
	Failed[a]		Disturbed[b]		Successful		Destroyed by weather		
Month	N	%	N	%	N	%	N	%	Total
May									
Visited nests	13	33	7	17	20	50	0	0	40
Unvisited nests	10	25	2	5	27	68	1	2	40
June									
Visited nests	10	25	4	10	26	65	0	0	40
Unvisited nests	7	18	4	10	25	62	4	10	40
July									
Visited nests	5	12	1	2	33	84	1	2	40
Unvisited nests	5	12	5	12	28	71	2	5	40
Total	50	21	23	10	159	66	8	3	240

[a] Failed = two eggs missing after 6 days.
[b] Disturbed = one egg missing after 6 days.

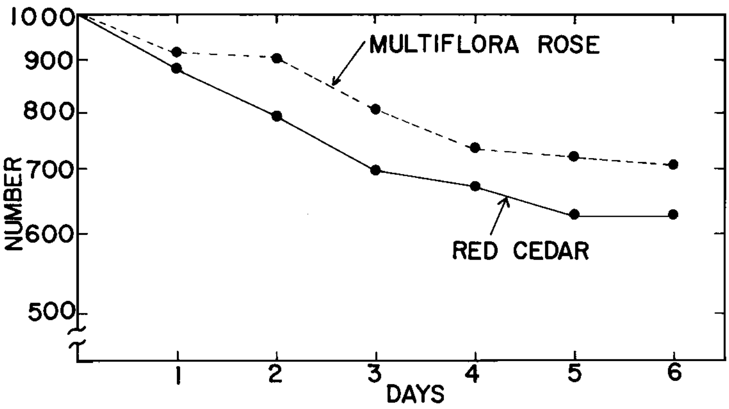

Fig. 3. Survivorship curves of visited experimental nests in multiflora rose and red cedar; data from all months pooled.

nest in the nearest site that appeared suitable. This insured even dispersion of nests throughout the study area each week.

Experimental nests were placed in sites that we think closely resembled nest sites of Cardinals, chats, Mourning Doves, and Field Sparrows. Most frequently selected sites were in multiflora rose, red cedar, and on the ground at the base of small cedars and saplings. After placing each elevated nest in position, the junior author estimated its degree of concealment to the human eye. Nests were ranked as concealed (rank = 2), intermediate (1), or exposed (0) from each of three perspectives, viz., above, below, and to the sides. Rankings of the three positions were summed to give concealment ratings for all elevated nests. Completely concealed nests were rated as 6, totally exposed nests as 0.

On finding an experimental nest with one or both eggs missing, we examined the nest and ground below to determine if wind had dumped the contents. If so, the nest is excluded from all analyses. All other nests that lacked eggs are classified as preyed upon (Nolan 1963, Thompson and Nolan 1973), since it is unlikely that Brown-headed Cowbirds (*Molothrus ater*) took any of the missing eggs (Thompson and Gottfried 1976).

While the experiment was being performed, we also followed the nest success of birds breeding on the study area. All natural nests were visited daily and the eggs in each were handled in the same way as in the experimental nests. To calculate success of these natural nests, we used only those found before the last egg of the clutch was laid. Although this decreases our sample of natural nests, it eliminates the bias toward success that comes from including nests found at different stages of the nesting cycle (Mayfield 1961; 1975; Nolan 1963). Of the 30 natural nests studied, 10 each were found in May, June, and July.

The following subsamples and terms are defined for analytical purposes: (1) For comparisons of visited vs. unvisited and experimental vs. natural nests, nests that lost one egg (disturbed) or both eggs (failed) are pooled as having been taken by a predator. (2) For comparisons of durations of survival of nests and for construction of survivorship curves both disturbed and failed nests are used; when nests failed but eggs disappeared on different days, we calculated failure as occurring on the date the first egg disappeared. The figure used for the time of failure was 0.5 days before the day the failure was discovered.

RESULTS

Seasonal predation trends.—Predation of experimental nests was highest in May (41%) and declined through June (33%) and July (21%). Although the monthly survivorship curves of the visited experimental nests differ greatly, the approximately straight lines obtained for May and July indicate a constant rate of predation throughout the 6 days of exposure (Fig. 2). Visited June nests, however, suffered no losses after their third day of exposure. The mean length of survival of experimental nests suffering predation did differ significantly between months (May $\bar{x}$ = 2.5 days, June $\bar{x}$ = 1.6 days, July $\bar{x}$ = 2.7 days; Kruskal-Wallis test, $H = 124.25$, $P < 0.05$).

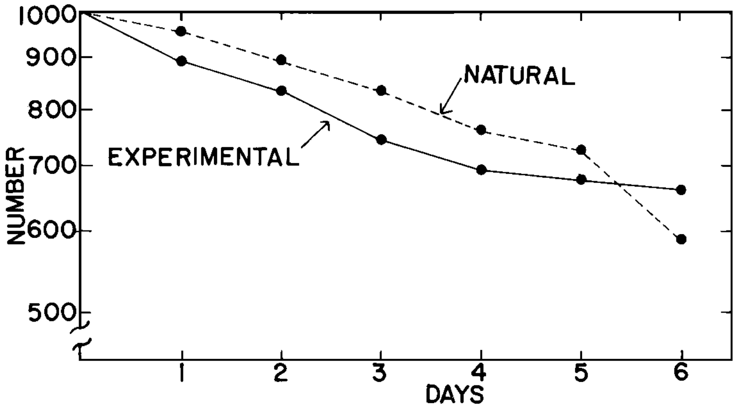

Fig. 4. Survivorship curves of visited experimental and natural nests; data from all months pooled.

Effect of observer visits.—To determine whether observer activity affected the chance that a predator would take the eggs, data on predation of visited nests are compared with those for unvisited experimental nests (Table 1). There were no differences either for the season as a whole (adjusted χ^2 test, $\chi^2 = 0.34, P > 0.05$) or for any month (May $\chi^2 = 2.28$, $P > 0.05$; June $\chi^2 = 0.03$, $P > 0.05$; July $\chi^2 = 0.81, P > 0.05$). Thus daily visits to nests did not significantly increase predation rates.

Effect of concealment and site.—Concealment ratings of 68 elevated nests taken by predators did not differ significantly from ratings of 137 successful elevated nests (successful median = 3.0, unsucessful median = 3.0; Mann-Whitney *U*-test, $U = 3926$, $P > 0.05$). Furthermore, the length of survival of 26 visited elevated nests that lost both eggs was not correlated with their concealment ratings (Kendall's tau = 0.12, $P > 0.05$).

The numbers of experimental nests taken by predators in multiflora rose and red cedars did not differ significantly for the season ($\chi^2 = 1.89$, $P > 0.05$) or for any month (May $\chi^2 = 1.64$, $P > 0.05$; June $\chi^2 = 1.06$, $P > 0.05$; July $\chi^2 = 0.01$, $P > 0.05$) (Table 2). Nor did duration of survival of visited nests that were taken differ significantly between multiflora rose and red cedar nests (cedar median = 1.5 days; multiflora rose median = 2.5 days; $U = 149.5, P > 0.05$). Inspection of survivorship curves of nests in the two substrates suggests that the failure rate was constant and therefore independent of the duration of exposure (Fig. 3).

Numbers of elevated and ground experimental nests preyed upon were not significantly different ($\chi^2 = 1.41, P > 0.05$). Duration of survival of ground and elevated experimental nests suffering predation cannot be compared because of the small sample size of visited ground nests.

Comparison between experimental and natural nests.—To approach the problem of whether nest failure is related to parental activity, visited experimental nests (no parental activity) and visited natural nests (parental activity) are compared. Because of the 6 day period of our experiments, only the first 6 days after discovery of the natural nests are considered. Twelve of 30 natural nests (40%) and 40 of 119 experimental nests (34%) were taken; this difference is not statistically significant ($\chi^2 = 0.19$, $P > 0.05$). Similarily, the duration of survival of experimental nests preyed upon (median = 2.5 days) and of natural nests (median = 2.5 days) did not

TABLE 2. The outcome of experimental nests in relation to nest site. Visited and unvisited nests are pooled

	Preyed upon								
	Failed		Disturbed		Successful		Destroyed by weather		
Month	N	%	N	%	N	%	N	%	Total
May									
Elevated nests									
Multiflora rose	7	22	4	12	20	63	1	3	32
Cedar	14	42	3	9	16	49	0	0	33
Other[a]	1	50	0	0	1	50	0	0	2
Ground nests	1	8	2	16	10	76	0	0	13
June									
Elevated nests									
Multiflora rose	5	14	5	14	24	64	3	8	37
Cedar	10	36	2	7	15	54	1	3	28
Other[a]	1	17	0	0	5	83	0	0	6
Ground nests	0	0	1	11	8	89	0	0	9
July									
Elevated nests									
Multiflora rose	6	16	3	8	26	68	3	8	38
Cedar	3	9	3	9	26	82	0	0	32
Other[a]	1	20	0	0	4	80	0	0	5
Ground nests	1	20	0	0	4	80	0	0	5
Totals									
Elevated nests									
Multiflora rose	18	17	12	11	70	65	7	7	107
Cedar	27	29	8	9	57	61	1	1	93
Other[a]	3	23	0	0	10	77	0	0	13
Ground nests	2	7	3	11	22	82	0	0	27

[a] Other includes blackberry (*Rubus* sp.), hawthorn (*Crataegus* sp.), honeysuckle (*Lonicera* sp.), etc.

differ significantly ($U = 312.0$, $P > 0.05$). The survivorship curves of both visited experimental and of natural nests suggest that likelihood of failure was independent of duration of exposure (Fig. 4).

DISCUSSION AND CONCLUSIONS

Predation of the experimental nests follows the pattern observed for natural nests in other old-field habitats (Nolan 1963, Thompson and Nolan 1973) as well as for natural nests found on the Bachelor Estate (Fig. 4, Thompson and Gottfried unpubl. data). Although we estimate that our placement of experimental nests approximately doubled the density of nests on the study area, we saw no evidence that this attracted unusual numbers of predators. Since circumstances of disappearance of eggs from both natural and experimental nests were indistinguishable, we think that conclusions derived from the use of experimental nests can be applied to natural nests.

Observer activity.—No statistically significant differences were found in any comparison of visited and unvisited nests. Only in May was there an appreciable, but still statistically insignificant, difference in proportions of visited and unvisited nests that failed. Both Stoddard (1931: 195) and Klimstra and Roseberry (1975: 31), who studied the ground-nesting Bobwhite (*Colinus virginianus*) in habitat similar to ours, found no evidence that nest visits by observers affected the chance that a nest would be destroyed by a predator. Roseberry and Klimstra (1970: 258) reached the same conclusion after visits to Eastern Meadowlark (*Sturnella magna*) nests, and Willis' (1973) elegant indirect observations on visited and unvisited nests of Bicolored Antbirds (*Gymnopithys bicolor*) in tropical rainforest also revealed no differences.

In old fields, mammals, birds, and snakes are predators of eggs and nestlings. Nolan (1963, unpubl. data), Thompson and Nolan (1973), and Thompson (unpubl. data) have observed several species of snakes, Blue Jays (*Cyanocitta cristata*), and eastern chipmunks (*Tamias striatus*) take eggs and young from nests in Indiana and Georgia old fields. We saw few chipmunks on the Bachelor Estate. However, black rat snakes (*Elaphe obsoleta*), other snakes, and Blue Jays were abundant and probably were responsible for most egg losses. These predators, unlike larger mammals, take only contents and leave the nest intact (Nolan 1963, Thompson and Nolan 1973), which was the condition of the large majority of our natural and experimental nests suffering predation.

Of the potential predators, mammals are the most likely to find nests by noting human activity or by following trails (Earl 1950, Willis 1973). However, Stoddard (1931: 195) makes an important point about predators' using human activity to find nests, ". . . [where] the whole terrain is daily crisscrossed by the trails of people going about their work afield . . . there would be no conceivable gain for any creature to follow out these countless trails." Blue Jays also might use cues left by humans (cf. Picozzi 1975), but in our opinion snakes would be less likely to do so. As most predators on our nests probably were snakes and, perhaps, Blue Jays, the lack of difference between visited and unvisited nests is not unexpected.

Two features of the design of our experiment should be kept in mind when considering the results. First, each experimental nest was exposed to predators for only 6 days, to avoid spoilage of the eggs. Daily visits over longer periods might increase the likelihood of their discovery. If this were true, however, one would expect natural nests to experience higher daily failure rates after 6 days and, probably, an increase in daily failure rates during the first 6 days; neither of these expectations was fulfilled (see also Mayfield 1975, Thompson and Nolan 1973, Willis 1973). Second, we went to each unvisited nest once, of course, to set it in place. One visit might attract predators just as readily as many visits. But this seems likely to be true only of mammalian predators using scent trails, and we think that it is not applicable to old-field habitats and can be ignored.

Why are some nests preyed upon?—Elimination of questions of the potential effect of observer visits clarifies consideration of other factors that contribute to discovery of nests by predators. Despite the obvious selective value that predator-avoidance adaptations must have for open-nesting birds facing heavy predation, remarkably little attention has been given to such adaptive responses. Use of experimental nests is ideal for such investigations, as one can have large sample sizes and can easily manipulate nest site characteristics.

An obvious hypothesis is that poorly concealed nests are more easily found by predators than are well concealed nests. Nice (1937: 93–94) and Nolan (1977) reported that nests of Song Sparrows and Prairie Warblers (*Dendroica discolor*), respectively, rated by them as poorly concealed were indeed more easily found by predators, but Roseberry and Klimstra (1970: 246) found no relationship between concealment and nest success in Eastern Meadowlarks. Dwernychuk and Boag (1972), using a visual rating system, found no relationship between egg loss and concealment in natural duck nests, but did find an inverse relationship in artificial nests. Cryptically colored eggs of Black-headed Gulls (*Larus ridibundus*) survived significantly longer than exposed or white eggs (Tinbergen et al. 1967). Our results provide no evidence that better concealed nests (to the human observer) suffer less predation: Concealment ratings of preyed upon and successful experimental nests are not significantly different, nor is the duration of survival of nests suffering predation correlated with concealment rating. This was unexpected and may be due, of course, to the crudeness of the visual rating system and analysis. If, however, the results are correct, they suggest that predators do not find nests by simple visual searches, but rather employ subtler means.

Absence of differences in predation of nests in red cedar and multiflora rose was unexpected. Based on past experience in other old-field habitats, we anticipated that few natural nests would be built in red cedars during June and July, when deciduous plants provide adequate nesting cover. If predators focus searching activities on vegetation types in which nests are most frequent, nests in red cedar would be less likely to be taken than those in multiflora rose during June and July. That no difference occurred may have been the result of selection of nest sites in red cedar throughout June and July by Mourning Doves and, unexpectedly, Cardinals and Field Sparrows. Natural nests were probably sufficiently numerous in both coniferous and deciduous sites all summer to keep predators searching in both.

The suggestion that predators find nests by being attracted to parental activity appears to be widely accepted (Skutch 1949, Hammond and Foreward 1956, Willis 1973), although Ricklefs (1969: 6) pointed out that his survey of the literature on nest success produced little evidence to support the hypothesis. Neither did our results support it. Experimental nests suffered approximately the same loss as natural nests built and attended by parents. Of course, our experimental nests may have been more poorly concealed than natural nests, and deficient concealment may have offset the attraction of parental activity to natural nests. However, although we did not give concealment ratings to natural nests, it seems unlikely that experimental nests were regularly more poorly concealed than natural nests. Furthermore, the demonstrated lack of correlation between concealment and survival of experimental nests suggests that concealment may not strongly affect nest success.

The design of this experiment does not allow further investigation of possible cues that predators use to find nests. More experimental work in old-field habitats is needed to examine the roles played by concealment, olfaction, and nest site in determining nest success.

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EVOLUTION IN THE HOUSE SPARROW—VI. VARIABILITY AND NICHE WIDTH

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ABSTRACT.—Degree of secondary sexual size dimorphism in House Sparrows, *Passer domesticus*, varies from small at low latitudes to large at high latitudes. This organization of size dimorphism is an expression of geographic variation of locality variance in body size. For North American populations variance in body size is inversely correlated with number of interspecific competitors, and may result from the interplay between interspecific competition tending to decrease size variation and intraspecific competition tending to increase size variation. For European populations variance in body size is inversely related to number of congeneric species of *Passer*, but possible causal factors seem to be more complicated than they are for North American House Sparrows. Nevertheless, in either set of continental populations, degree of body size variation at a locality may reflect relative niche width. *Received 12 July 1976, accepted 30 November 1976.*

STUDIES associating morphologic structure of organisms with ecologic structure in environments have approached the topic from many angles, and apart from the more strictly paleontologic (Ashton and Rowell 1975) include those that correlate anatomic parts with prey size (Hespenheide 1966, 1973; Pulliam and Enders 1971; Willson 1971; Willson and Harmeson 1973), that assess interspecific competition and food availability (Lack 1947, MacArthur 1972, Soulé 1966, Schoener 1970), that emphasize relative abundance of conspecifics (Van Valen 1973), that predict competitor coexistence (e.g. Pulliam 1975), and that relate morphologic variance to niche width (e.g. Van Valen 1965, Rothstein 1973). We think comparisons of morphologic variation in populations of House Sparrows, *Passer domesticus*, in Europe and North America provide additional insight concerning the adaptive interplay between morphology and environment as this is mediated by intra- and interspecific competition. In particular, we wish to examine geographic variation in degree of secondary sexual size dimorphism (Johnston and Selander 1973) that is expressed in clinal trends of variance in overall size in putative accord with variation in niche width.

SAMPLES, TECHNIQUES, AND METHODS

The data are skeletal measurements of 1,571 House Sparrows from 14 North American localities and 842 specimens from 22 European localities (Table 1). In North America, elevations of sample sites range from sea level to 1,260 m. All sites except one are in prairie or grasslands to maximize environmental, or habitat, similarities and minimize altitudinal differences. Oaxaca, Mexico is not representative of grasslands but is used because it has the lowest elevation of the extreme southern populations with specimen data. In Europe, localities encompass a wider variety of habitats but a smaller range of altitudes, between sea level and 1,000 m. All data were extracted from a larger data matrix assembled by the junior author (cf. Johnston and Selander 1973).

Fourteen skeletal measurements per specimen are the bases from which overall body size is determined; the 14 were measured according to Johnston and Selander (1971), but narial width and femur width were omitted. A subset of skeletal measurements, consisting of skull width and length, premaxilla, dentary, and mandible lengths, provide the input for calculating "bill size." All measurements of "bill size" deal with the morphology of selecting, cracking, and ingesting seeds. Skull length and width are included, since they provide information on muscle attachments, critical factors in granivory. All specimens were collected between 1962 and 1972.

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TABLE 1. Skeletal samples of House Sparrows used in this study

			Number of specimens	
Locality	Latitude	Year collected	Female	Male
		North America		
Peace River, Alberta	56.25	1972	12	14
Edmonton, Alberta	53.57	1963	45	45
Sisseton, South Dakota	45.65	1967	15	27
Manhattan, Kansas	39.18	1971	91	119
Quinter, Kansas	39.07	1966	16	18
Topeka, Kansas	39.03	1966	73	76
Lawrence, Kansas	38.97	1962–70	141	281
Hays, Kansas	38.88	1968–69	81	90
Kit Carson, Colorado	38.75	1968–69	84	97
Udall, Kansas	38.00	1967	14	35
Bastrop, Texas	30.12	1962	22	47
Houston, Texas	29.75	1962	27	61
Progreso, Texas	26.50	1962	12	7
Oaxaca, Oaxaca	17.08	1963	10	11
		Total	643	928
		Europe		
Oslo, Norway	59.93	1970	9	11
Ostermalma, Sweden	58.83	1969	7	7
Aarhus, Denmark	56.17	1969	15	12
Malmö, Sweden	55.58	1970	34	28
Warsaw, Poland	52.83	1964	28	16
Oxford, England	51.77	1962	52	57
London, England	51.50	1969	25	15
Mainz, Germany	50.00	1969	8	5
Oberstenfeld, Germany	48.90	1962	20	19
Ludwigsburg, Germany	48.90	1962	26	41
Paris, France	48.86	1969	18	18
Stuttgart, Germany	48.78	1962	24	15
Radolfzell, Germany	47.73	1969	16	14
Sempach, Switzerland	47.22	1970	21	25
Geneva, Switzerland	46.22	1969	7	19
Karlovač, Yugoslavia	45.50	1970	9	8
Mantova, Italy	45.17	1965	17	27
Parma, Italy	44.80	1965, 70	14	14
Comacchio, Italy	44.70	1965	18	26
Titograd, Yugoslavia	42.47	1970	8	16
Cantalupo Sabino, Italy	42.30	1965	8	16
Cagliari, Sardinia	39.22	1965	23	26
		Total	407	435

Both multivariate (principal component, discriminant function, and multiple regression) and bivariate (linear regression and correlation) analyses were applied to European and North American characters and character sets. Principal component (PC) analysis provides an analytical technique for detecting morphologic covariation in characters and produces factors that represent linear combinations of an original suite of variables. The variation explained by the 14 skeletal measurements is expressed through PC analysis by 14 eigenvectors that are orthogonal to one another (lacking statistical correlation).

Principal component analysis based on the variance-covariance matrix was applied to both the original 14 variables of body size and the 5 variables of bill size; the two sexes were analyzed separately and combined. In all instances PC I appears to represent size variation (Tables 2 and 3), since character loadings tend to make equal contributions to the first eigenvector and are of the same sign (Morrison 1967, Blackith and Reyment 1971). Standard statistics, including mean and variance of PC I scores, were then calculated for each locality; correlation between locality variances of PC I scores and latitude was tested using Spearman's rank correlation analysis. Stepwise multiple regression analysis was performed on data sets from each continent separately, testing the ability of mean PC I scores and latitude to explain variation in locality variance of PC I scores. Partial correlations from multiple regression were used to determine whether change in variance of body size merely reflects change in average body size.

Most computations were done at The University of Kansas Computation Center; later revisions were conducted at the University of Maryland Computation Center. Programs employed include NT-SYS (Rohlf et al. 1969), UNIVAR (Power MS), and SPSS (Nie et al. 1970).

TABLE 2. Character loadings from variance-covariance matrices onto the first Principal Component in a 14-character set of skeletal variables from North American and European House Sparrows. F = females, M = males

Variable	North America[a]			Europe[b]		
	F	M	F + M	F	M	F + M
Premaxilla length	0.115	0.120	0.111	0.138	0.154	0.137
Cranial width	0.151	0.155	0.174	0.191	0.186	0.199
Skull length	0.390	0.396	0.380	0.493	0.563	0.518
Dentary length	0.111	0.125	0.114	0.128	0.149	0.135
Mandible length	0.294	0.304	0.282	0.382	0.378	0.366
Coracoid length	0.412	0.404	0.432	0.494	0.472	0.514
Sternum length	0.482	0.492	0.560	0.681	0.683	0.731
Keel length	0.523	0.612	0.704	0.741	0.754	0.854
Sternum depth	0.210	0.246	0.271	0.276	0.263	0.290
Humerus length	0.437	0.380	0.428	0.523	0.502	0.527
Ulna length	0.479	0.459	0.534	0.607	0.576	0.654
Femur length	0.570	0.387	0.441	0.501	0.483	0.480
Tibiotarsus length	0.732	0.770	0.716	0.883	0.828	0.838
Tarsometatarsus length	0.584	0.522	0.520	0.668	0.645	0.646
% of variation explained by PC I	45.1	51.1	49.4	59.0	60.6	60.4

[a] ♀♀, N = 643; ♂♂, N = 928.
[b] ♀♀, N = 407; ♂♂, N = 435.

RESULTS

Variance in body size.—House Sparrow populations show greater variation in body size at northern latitudes and are more homogeneous in size in the south. This clinal pattern is supported by positive correlation between the variance of PC I scores depicting overall size of the pooled sexes (here called PC I variance) and latitude in both North America ($r_s = 0.807$; $n = 14$; $P \leq 0.01$) and Europe ($r_s = 0.423$; $n = 22$, $P \leq 0.05$).

Stepwise multiple regression indicates that latitude contributes more to the explanation of variation in PC I variance than does the mean of PC I scores describing overall size (hereafter called PC I mean). In both North American and European data sets, latitude is the first variable to enter stepwise multiple regression (0.001 = tolerance, 0.01 = F to enter) followed by the second and final variable PC I mean. Latitude explains 62.9% ($R^2 = 0.629$) of PC I variance in North American and 18.1% in European samples. PC I mean accounts for a proportionate increase in explained variation of 3.2% and 10.5% in the respective continental data samples. This increase is determined from the squared partial correlation coefficients.

Because average body sizes of House Sparrows increase clinally with increasing latitude in North America (Johnston and Selander 1973) it was possible that clinal increase in body size variance simply reflected increase in overall size. A higher correlation between PC I variance and latitude than between PC I variance and PC I mean within the North American populations suggests factors other than mean body size produce the latitudinal gradient of variance in body size. In European House Sparrows a significant positive latitudinal cline in body size variance occurs despite a negative latitudinal cline in mean body size (Johnston and Selander 1973).

Spearman's correlation between PC I variance and latitude for males and females separately within their respective continental samples produces a significant relationship ($P < 0.05$) in only one case. North American females correlate positively with latitude ($r_s = 0.728$; $n = 14$; $P \leq 0.01$) and adhere to the general pattern of increased variation in body size within House Sparrow populations at higher latitudes.

TABLE 3. Character loadings from variance-covariance matrices onto the first Principal Component in a five-character set of skeletal variables associated with feeding from North American and European House Sparrows

	North America[a]			Europe[b]		
Variable	F	M	F + M	F	M	F + M
Premaxilla length	0.208	0.214	0.211	0.233	0.235	0.234
Cranial width	0.178	0.184	0.186	0.154	0.192	0.178
Skull length	0.575	0.564	0.569	0.751	0.703	0.726
Dentary length	0.183	0.196	0.191	0.194	0.213	0.204
Mandible length	0.461	0.447	0.453	0.510	0.529	0.521
% of variation explained by PC I	69.7	72.4	70.8	69.1	73.7	71.2

[a] ♀♀, $N = 643$; ♂♂, $N = 928$.
[b] ♀♀, $N = 407$; ♂♂, $N = 435$.

Bill size variation.—Continental differences between House Sparrows appear in geographic patterns of bill and cranial measurements. In European samples variance of PC scores derived from bill and skull measurements of the pooled sexes (hereafter called BS I variance) correlates positively with latitude ($r_s = 0.555$; $n = 22$; $P \leq 0.01$), but means of the same PC scores (hereafter called BS I mean) describe a negative association (BS I $\bar{x} = 1.76 - 0.035$ lat., $P \leq 0.008$). Neither BS I variance nor BS I mean correlate significantly with latitude in North American samples ($r_s = 0.035$; $n = 14$; $P > 0.05$; BS I $\bar{x} = 0.077 - 0.004$ lat., $P = 0.514$).

The most pronounced clinal variation in bill variance occurs in samples in which sexes are pooled, and not within each sex. Correlations relating BS I variance to latitude for males and females separately are not statistically significant ($P > 0.05$). This observation holds for both Old and New World samples.

Sexual differences.—Differences between the sexes are reflected in mean bill size on each continent. Average bill size in males follows a strong cline along a latitudinal gradient, but latitudinal trends in female bill size are weak and statistically nonsignificant. Geographic change in average bill size is directly correlated with the change in mean body size. Both average body and bill sizes in males increase with increasing latitude in North America (BS I $\bar{x} = -0.981 + 0.027$ lat., $P \leq 0.01$) and decrease with increasing latitude in Europe (BS I $\bar{x} = 1.67 - 0.036$ lat., $P \leq 0.02$).

COMPETITION AND VARIATION IN NICHE WIDTH

Bill size and body size both have been used by ecologists as indicators of prey size. Larger-billed birds generally take larger items of food than smaller-billed birds (Hespenheide 1966, Myton and Ficken 1967, Newton 1967, Willson 1971). Larger-bodied individuals generally select larger food items than smaller-bodied individuals (Pulliam and Enders 1971, Brown and Lieberman 1973; for literature review see Hespenheide 1973: 216). Population variance in body size and/or bill size may indicate the range in size of food items taken by individuals in a population, in other words, intraspecific competition (within-phenotype competition) bears on niche size—stiff competition will tend to increase niche width.

Range in prey sizes selected by House Sparrows is in turn influenced by the distribution and abundance of other taxa—we note the dependence on plant productivity (House Sparrows are mostly granivorous in winter) and the influence of interspecific competition. Under heavy competitive pressure from other granivores the variety of seed sizes available to House Sparrows, and thus niche width, may be reduced. But, to the point, we suggest that reduction in the size range of available foods results in reduced variance of House Sparrow body or bill size. Support for this contention is found in the differential occurrence of potential competitors along a north–south continental transect. And, as we will show beyond, interspecific competition correlates inversely with latitude and inversely with degree of variability in overall size of House Sparrows.

Pianka (1966) noted that interspecific competition is likely to vary with latitude. In modeling variation in food abundance for a species, Lack (1947), Van Valen (1965), Willson (1969), and Rothstein (1973) were prepared to believe that relative food abundance diminishes where number of congeneric species increases. In western Europe there are three species of *Passer* (Summers-Smith 1963), but only *P. domesticus* occurs effectively in North America (populations of *P. montanus* occur in low densities around St. Louis, Missouri—e.g. Anderson 1973). Possible competitive pressure in North America is applied by a variety of granivorous birds that variously share House Sparrow habitats and, in effect, replace the pressure of congeneric competitors.

The competition index.—A competition index, C, was designed to test for variation in competitive pressure and to measure interspecific competition at specific localities, differentially weighting the effects of competing species. A comparison of C-indices from localities differing latitudinally provides a technique to detect latitudinal change in competitive pressure. The C-index takes the form:

$$C = \sum_{j=1}^{n} w_j d_j N_j,$$

where C = locality interspecific competition index, n = total number of competing species, w_j = average body weight of species j, d_j = fraction of diet in species j identical to that of *P. domesticus*, and N_j = total number of individuals of species j.

Competing species possessing numerous individuals (large N), sharing a large fraction of the House Sparrow diet (large d), and maintaining a large body size (large w) contribute heavily to competitive pressure; small, rare species with marginal dietary overlap with *P. domesticus* add little to the pressure of interspecific competition and to the C-index. A large C value indicates that House Sparrows at a given locality can experience appreciable interspecific competition.

In testing competition, only North America was considered, since necessary census data were not available for Europe. Competing species included only those that share all or part of the House Sparrow habitat (Table 4) and feed on at least one of the kinds of seeds listed by Martin et al. (1961) as comprising the wintertime diet for prairie House Sparrows—bristlegrass, corn, crabgrass, elm, knotweed, oats, ragweed, smartweed, sorghum, and sunflower. Average weights of species were obtained from Tordoff and Mengel (1956), direct field measurements (Peter Lowther, unpubl. data) and average weights of museum specimens in The University of Kansas Museum of Natural History. Competitors' diets were derived primarily from Martin et al. (1961), but see Table 4.

Number of individuals for each competing species was calculated by averaging observations from the 1967 and 1968 Christmas Bird Counts (Cruickshank 1967, 1968). The number of individuals per species was divided by party hours for each locality; species represented by seven individuals or less were omitted to eliminate bias favoring sightings of rare birds. Initially, total number of competing individuals

TABLE 4. House Sparrow competitors, average competitor weights, and percent of competitor diets identical to that of *P. domesticus*

Potentially competing species	Average weight (g)	References for weight[a]	% diet identical to House Sparrows[b]
Starling, *Sturnus vulgaris*	95	M	2
Evening Grosbeak, *Hesperiphona vespertina*	55	M	5
Snow Bunting, *Plectrophenax nivalis*	35	M	60
Black-billed Magpie, *Pica pica*	150	T	15[c]
Common Redpoll, *Carduelis flammea*	14	M	60
Harris' Sparrow, *Zonotrichia querula*	36	L	75
Pine Siskin, *Carduelis pinus*	18	L	5
Common Grackle, *Quiscalus quiscula*	100	L	65
Dark-eyed Junco, *Junco hyemalis*	22	L	30
Field Sparrow, *Spizella pusilla*	14	M	30
Cardinal, *Cardinalis cardinalis*	48	L	12
Song Sparrow, *Melospiza melodia*	20	T	60
White-throated Sparrow, *Zonotrichia albicollis*	26	L	60
White-crowned Sparrow, *Zonotrichia leucophrys*	25	M	70
Common Crow, *Corvus brachyrhynchos*	475	M	50
Tree Sparrow, *Spizella arborea*	19	M	37
Mourning Dove, *Zenaida macroura*	130	M	55
American Goldfinch, *Carduelis tristis*	15	L	20
Brown-headed Cowbird, *Molothrus ater*	45	M	55
Red-winged Blackbird, *Agelaius phoeniceus*	60	M	50
Savannah Sparrow, *Passerculus sandwichensis*	18	T	30

[a] M = mean weight of five specimens (Museum of Natural History, KU); T = Tordoff and Mengel (1956); L = Peter Lowther (unpublished).
[b] From Martin et al. (1961).
[c] From Kalmbach (1927).

divided by party hours and a C-index were calculated for 14 North American and Canadian localities, comprising a latitudinal transect through the Great Plains. Regressions of individual competitors on latitude and of the C-index on latitude are significant (*Number of competitors* $= 93.5 - 1.89$ lat., $P < 0.01$; $C = 245 - 5.02$ lat., $P < 0.01$).

Because localities of Christmas bird counts and our collecting localities were not identical, C-index was computed for 12 new localities with latitudes and habitats comparable to those of specimen sites. No data were available for latitudes corresponding to Peace River, Alberta or Oaxaca, Mexico. Correlation of body size variance on the C-index indicates a strong inverse relationship (Fig. 1); variance in body size is maximal where interspecific competition appears to be least ($r_s = -0.802$; $n = 12$; $P \leq 0.01$).

METHODOLOGICAL NOTES

An important focus of this study has been on the relationship between morphometric character variance and within- and between-species competition. This relationship allows us to approach the core of the niche-variation hypothesis, which states that the amount of within-population character variance is directly proportional to niche width of the population, assuming that variation in competitive pressure will be reflected in variation in niche width (Van Valen 1965, Soulé and Stewart 1970, Rothstein 1973). Our examination within the confines of one species shows significant variation in character variances for both overall size and size of the feeding structures, significant variation in the probable degree of interspecific competition with House Sparrows from other avian granivores, and a significant negative correlation between character variance and interspecific competition. Finally, if some

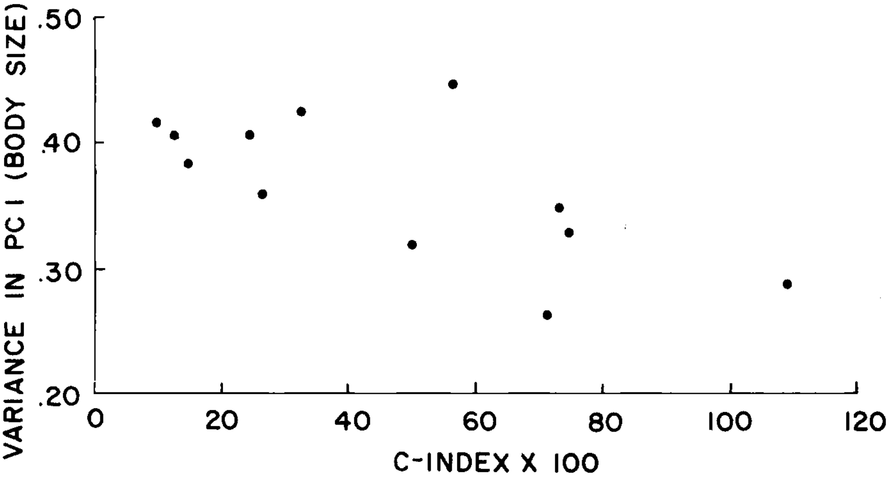

Fig. 1. Variance in Principal Component I (PC I, overall body size) of North American House Sparrows plotted on an index to interspecific competition for food (*C*-index). PC I scores closely approximate body size and were computed from 14 skeletal variables of males and females combined. A large *C*-index indicates potentially intense interspecific competition. Spearman's correlation coefficient between variance in body size and the *C*-index is $r_s = -0.802$ ($P \leq 0.01$; $n = 12$).

dimensions of niche width are conceded to vary in accord with the amount of interspecific competition, then this instance of House Sparrow morphometrics supports the niche-variation hypothesis. An assessment of the strength of this support includes the following, largely methodological, points.

Estimating character variances.—We computed variances for locality specimen sets for PC scores that summarized either five cranial (feeding) dimensions or 14 (overall size) dimensions. Both sets of characters are larger than most such sets employed in examining the niche-variation hypothesis, and the number of specimens is likewise robust. Hence, our estimates of character variances are likely to contain information on lability in feeding apparatus in a much more complete way than is usual, especially since many studies use only bill and tarsus measurements.

Body size in House Sparrows in North America varies from large in the north to small in the south, and since variance scales on size we expected to find parallel variation in variance estimates. Tests for such influence showed it to be of small importance. Fortunately in this regard, body size of European House Sparrows varies from small in the north to large in the south and likewise inversely to size variance. We are satisfied that our variance estimates are free of scaling influences.

Specific unit of analysis.—Our study is done on specimens referable to one species, and this is a departure from most other such analyses based on bird specimens. Since the evolutionary processes lying back of any instance of niche-variation conformity necessarily occur within a species (population), such a taxonomic focus is ideal for our purposes.

Habitat diversity and niche width.—Our specimen samples come from rural, predominantly farmyard, populations. The range in physical habitats sampled is relatively trivial and, although we make no attempt to estimate the range, it is certainly less than that found in species not so strongly commensal with humans. Biotic components of the habitats vary more than physical aspects, and one such source of variation is optimal—wintertime variation in number of granivorous competitors. Another source of variation in habitat is less than ideal, however, and this is that owing to differences in sizes of seeds available to the granivores; such variation can almost never be controlled and is an appreciable source of error in this study.

Temporal diversity and niche width.—The specimen samples were largely netted from fall and winter flocks; most samples were secured prior to mid-winter of any year. Since sparrow populations are known to vary significantly in morphometrics over the winter period (the Bumpus Effect; see Bumpus 1899; Johnston et al. 1972, O'Donald 1973, Johnston and Selander 1973), it is of some consequence to have samples as nearly time-constant as possible. Such time-constancy has been violated in taking some samples for use here, and this is a source of error tending to reduce the precision with which morphometric data can reflect relative niche size.

Granivory, wintertime, and the period of selection.—House Sparrows eat seeds at any time of year, but in winter they are nearly dependent on such food. The winter is also when very powerful selective pressures have been found to operate on size of sparrows (O'Donald 1973); such strong selection, and even lesser pressures (Rising 1973, Johnston and Selander 1973) are known to generate significant increases in degree of sexual dimorphism at a locality. Character variances likewise increase under such differential selection. Individual successes under such selection are partly determined by degree of intraspecific competition. If we now add consideration of interspecific wintertime granivory we should very nearly have touched the major forces generating variation in food aspects of niche width in House Sparrows. Similar views of wintertime as a major source of selective mortality are developed by Lack (1966) and Fretwell (1972).

Sensitivity of the C-index.—Our C-index explicitly considers only abundance, relative size, and degree of feeding overlap of actual or potential granivorous competitors, but there is implicit treatment of other aspects of interspecific competition. For example, competitive success among birds is frequently owing to large size. Thus it is that a starling (*Sturnus vulgaris*) can displace all House Sparrows at a feeding site simply by arriving and taking a perch; its size, large relative to a House Sparrow, seemingly is read as a guarantee of aggressive competitive vigor. The C-index of course includes size, so some weight is given to this aspect of the psychology of aggressive interaction.

Abundance of the potential granivorous competitor is judged by the wintertime censuses of birds taken by cooperators of the National Audubon Society, but not necessarily at the exact localities from which we obtained samples of sparrows.

DISCUSSION

Two aspects of niche width.—Niche width for a species is comprised of two aspects of variability—that for individuals (individual flexibility) and that for populations (differences between individuals in a population). Our information and our emphasis concern the latter, largely from a position of morphologic inference. The hard data are bony sizes of House Sparrows; this allows us to infer a part of the niche hypervolume for sparrows in general terms, but we nevertheless miss the information on individual flexibility.

We suppose that individual flexibility is likely to be a behavioral, not a morphologic, quality. This is not a polar dichotomy, for behavioral variables are often influenced by morphology, as when North American House Sparrows fight for position at a good foraging site in winter—large individuals win much more often than small ones, whether in Saskatchewan, North Dakota, Nebraska, or Kansas (C. L. Cink, pers. comm.). Even so, we have no way of knowing how much morphologic variation within populations is organized by behavioral interaction, and further assume that some behavioral flexibilities in individuals are neither mediated by nor translated into variation in morphology.

Our approach includes no direct behavioral information on House Sparrows, but we think that were we to have such information the precision with which we could track relationships between morphology and niche width should increase. And, perhaps the degree of scatter of points in Fig. 1 would be reduced if information on behavioral aspects of interspecific competition in House Sparrows were available.

Sociality and niche width.—Hespenheide (1975: 176) has supposed that "the normal means by which [intraspecific] competition is alleviated . . . [is] . . . by the social structure of the population." Furthermore, he notes that territorial species have social structures placing only paired males and females in competition with each other. He views such a problem of competition as being as readily soluble through behavioral and ecologic as through morphologic means. He goes on, "Only in species that feed in social groups on relatively rare food would differences in feeding (bill) morphology be useful in reducing intraspecific competition." Our information on House Sparrows can be taken as reasonable support for Hespenheide's hypothesis. Our information on morphologic differences transcends bill size, but we see no reason to modify the hypothesis. Additionally, food of House Sparrows during wintertime social feeding activities is not often "rare." Yet it is precisely at those times when most food is covered by snow that the advantages of differential size are greatest; it is then that most fighting for food occurs, and any means to feed successfully at opposite ends of a food spectrum would be of pronounced value for individuals. Realization of such value is highest at high latitudinal localities, owing to wintertime competitive release at those localities.

Significance of the European replication.—Because variation in body size of House Sparrows is clinally large to small from south to north in Europe (the opposite of what is found in North American populations), replication of the latitudinal increase in variance in size is extremely important. It not only vitiates any argument that the increase in variance is a mere effect of increase in body size, but also suggests that wintertime competitive release is exploited by different populations of House Sparrows in the same way, irrespective of body size.

Selection for variation in niche width.—The ultimate source of sexual size variation in House Sparrows probably involves Darwinian sexual selection. Phyletic considerations (Johnston and Klitz 1977) suggest the most recent ancestor of the House Sparrow was sexually dimorphic both in plumage and size, for its closest relative (*Passer hispaniolensis*) shares such sexual dimorphism. We envision sexual selection preceding any selection defining niche width—males became slightly larger than females owing to size advantages in intrasexual battles followed by female choice of winners as mates. Males were thus suited to using a larger range in seed sizes than females, who in turn could specialize on a set of smaller seeds. In this view males and females each comprise distinct selective populations, and each is a major component of the other's environment. Such a view also reduces the utility of earlier distinctions between "within-species" and "between-species" factors generating variation in niche width.

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A GUIDE TO FORMING AND CAPITALIZING COMPOUND NAMES OF BIRDS IN ENGLISH[1]

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THERE is much variation in usage, and much uncertainty among authors and editors (especially editors of nonornithological publications), with respect to the orthography of English names ("common names" or "vernacular names" of many authors, but see Parkes 1975: 819) when these names are compounded from two or more words. I refer only to the English group-name, not to the modifying word or words used to denote the particular species. Our concern here is with "Frigatebird" and not with "Magnificent."

The first modern attempt to standardize the orthography of the English names of North American birds was made by Cheesman and Oehser (1937), in a report originally prepared for the Committee on Classification and Nomenclature of the American Ornithologists' Union. The recommendations in their report dealt with several matters of orthography beyond those considered here.

Eisenmann (1955), in his paper on Middle American birds, "followed in the main" the recommendations of Cheesman and Oehser, and, in turn, most of the names used by Meyer de Schauensee (1966) were those recommended by Eisenmann as a consultant on English nomenclature. Even within these two works, however, the formation of compound names is inconsistent.

In spite of the editorial policies of some journals and book publishing companies, most ornithologists (including the writer) appear to believe firmly that the names of bird species should be capitalized. The usual reasons given for this, which are valid, are that it prevents the ambiguousness of such combinations as "gray flycatcher" and "solitary sandpiper," and that it makes the names of birds easier to spot in a page of print. In addition, the English name of a bird species can be considered to be a *proper name*, and thus entitled to capitalization (see editor's footnote in Cheesman and Oehser 1937: 335). Group-names in the plural are sometimes capitalized when they are intended as parts of two or more species names: thus, Common and Roseate Terns rather than Common and Roseate terns (U.S. Government Printing Office 1959: 22). However, the Council of Biology Editors prefers the second (uncapitalized) version (Council of Biology Editors 1972: 184), which should be used in manuscripts intended for biological journals.

When group-names are used alone in a textual context, whether single or compound, they are not capitalized. Thus we write, "The smallest of the hummingbirds is the Bee Hummingbird." Similarly, *Otus choliba* is the Tropical Screech-Owl, but there are several other species of *Otus* collectively called screech-owls (some of which are tropical screech-owls).

I developed the following "rules" during my attempt to standardize the nomenclature used in the "Avian Biology" series (Farner and King 1971–1975). They are intended as a kind of style manual; that is, guidelines for an approach to an almost complete consistency in the formation of compound names. Some are virtually unchanged from those of Cheesman and Oehser, and others attempt to codify the refinements made by Eisenmann and others. Adherence to these "rules" will, it is

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hoped, result in consistency of usage within journals and in ornithological works with multiple authorship.

I am indebted to Eugene Eisenmann, Chairman of the Committee on Classification and Nomenclature of the A.O.U., for having read several drafts of this paper; a number of his suggestions have been incorporated in this version. The Committee voted to adopt the "rules" in the A.O.U. Check-list, and has followed them in the published Supplements to the fifth edition. The manuscript was also read by Charles G. Sibley, whose forthcoming book on birds of the world will also reflect these "rules."

The "Rules"

I. Compound bird names should be spelled as **a single word, unhyphenated**, if:

A. The second component is the word "bird."

Examples: Tropicbird, Frigatebird, Oilbird, Hummingbird, Puffbird.

B. The second component is a part of the body.

Examples: Spoonbill, Pintail, Finfoot, Lapwing, Yellowlegs, Greenshank, Barbthroat, Violetear.

C. The name describes an activity of the bird (whether or not accurately!).

Examples: Shearwater, Roadrunner, Goatsucker, Honeyguide, Woodcreeper, Gnatcatcher, Seedeater.

D. The second component is a misnomer; either (1) a fanciful nonornithological noun, or (2) a group of birds to which the bird in question does not really belong.

Examples: (1) Woodnymph, Hillstar, Sunangel; (2) Sungrebe, Seedsnipe, Nighthawk, Antpitta, Fruitcrow, Peppershrike, Waterthrush, Meadowlark.

E. The second component is a broadly categorical bird name, not applying to any one particular kind of bird.

Examples: Moorhen, Guineafowl, Peacock and Woodcock, Bananaquit and Grassquit ("Quit" = old Jamaican word for a little bird; Newton and Gadow 1896: 761).

F. The name is onomatapoeic.

Examples: Bobwhite, Killdeer, Poorwill, Chickadee, Chiffchaff.

Exceptions: Names that would normally be spelled as single unhyphenated words under this rule should be spelled as **two (or more) hyphenated words, with only the first capitalized**, when:

(1) Spelling as a single word would result in a double or triple letter, from the juxtaposition of the last letter of the first word and the first letter of the second.

Examples: Thick-knee, not Thickknee (or Thicknee as in Williams 1963: 89); Bee-eater, not Beeeater; Whip-poor-will, not Whippoorwill; Swallow-wing, not Swallowwing; White-eye, not Whiteeye.

(2) An unhyphenated word would be excessively long (usually four syllables or more), or clumsy, or imply an incorrect pronunciation.

Examples: Plains-wanderer, not Plainswanderer; Chuck-will's-widow, not Chuckwill'swidow; Foliage-gleaner, not Foliagegleaner; Firewood-gatherer, not Firewoodgatherer; False-sunbird, not Falsesunbird; Silky-flycatcher, not Silkyflycatcher; Mudnest-builder, not Mudnestbuilder.

II. Compound bird names should be spelled as **two capitalized**, **hyphenated words**, if:

The second component is the name of a kind of bird, and is *not* a misnomer; i.e., the bird in question does belong to that general group. The first component may be a noun or an adjective.

EXAMPLES: Storm-Petrel, Diving-Petrel, Night-Heron, Whistling-Duck, Painted-Snipe, Ground-Dove, Screech-Owl, Wood-Wren, Bush-Shrike, Brush-Finch.

EXCEPTIONS: Some bird names that are technically of this kind have become ensconced in the English language as single nouns in their own right. As might be expected, these are names that were originally applied to British birds, viz. Sparrowhawk, Skylark, Stonechat, Goldfinch, Greenfinch, Bullfinch. In some, the first word has even evolved away from its original spelling, viz. Shelduck, Goshawk.

NOTES

There is obviously a subjective element in decisions as to what is awkward or excessively long and thus to be excepted from being spelled as a single word under Category I. Few cases, however, should present any difficulties of decision.

One special case is that of the group name for the Paradisaeidae. Ideally we should call these "Paradisebirds," but the inverted version is too firmly fixed to alter. I have seen the name rendered as "Bird of Paradise," "Bird of paradise," and "Bird-of-paradise"; I recommend the hyphenated form as used by Thomson (1964).

No compound group-name for a bird should be spelled as *two unhyphenated words*. In some instances this conflicts with A.O.U. Check-list usage, but not with that of Eisenmann; thus, "Night Heron" of the A.O.U. (1957) should be "Night-Heron." (On the other hand, "Great Blue Heron" and "Little Blue Heron" are unhyphenated, as there is no group of "Blue-Herons," both adjectives in these two names modifying the group-name "heron.") In a few cases, Eisenmann himself used unhyphenated words, but consistency would require that these be hyphenated. Thus "Black-Hawk" rather than "Black Hawk" should be used for the species of *Buteogallus*, congruent with Eisenmann's use of "Yellow-Finch" for the species of *Sicalis*. There is no justification for such a splitting as "oyster catcher" or "seed eater."

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A COMPARATIVE NESTING STUDY OF RED-TAILED HAWKS AND HARRIS' HAWKS IN SOUTHERN ARIZONA

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ABSTRACT.—I studied the nesting of Red-tailed Hawks in the Sonoran Desert of Arizona in 1969–1976, emphasizing its ecology relative to the Harris' Hawk, a species that I have found to be sometimes polyandrous and have nest helpers. Red-tails averaged 2.32 eggs per clutch (59 nests) and Harris' Hawks 2.96 (50 nests). The clutch size distributions of the two species were significantly different. Nest success was 81% for Red-tails and 68% for Harris' Hawks, but may actually be slightly lower because a nest was considered successful if a chick was raised to an age of at least 28 days but not always to fledging. For Red-tails, the average number of chicks produced was 1.55 per nest attempt (42 nests) and for Harris' Hawks 1.60 (50 nests). Red-tails nested exclusively in saguaro cacti, but the more agile Harris' Hawks used not only easily accessible saguaro sites but enclosed tree sites as well. Nest site availability seemed to have no significant role in population regulation. The nesting cycle of the Red-tailed Hawk, from egg laying to fledging, was from February to June; for Harris' Hawks it was from February to early December (because of second broods). Optimum habitat and greater hunting versatility in the Harris' Hawk may allow it a less restricted breeding season in saguaro-palo verde desert than the Red-tail by providing essential food resources. These two factors, and nest helping if it is common, probably contribute to maximizing the productivity of Harris' Hawks in an arid environment with variable food resources. *Received 2 June 1976, accepted 5 October 1976.*

THE Red-tailed Hawk (*Buteo jamaicensis*) has received little investigation in the southwestern deserts of the United States. This report presents information on the nesting ecology of this species in the Sonoran Desert of southern Arizona and compares it to that of the Harris' Hawk (*Parabuteo unicinctus*). Although both species are much the same size and occupy similar habitat in this desert, the Red-tailed Hawk is monogamous while the Harris' Hawk is at least in part polyandrous and has nest helpers. Recent evidence of pesticide contamination in the Red-tail (Seidensticker and Reynolds 1971) and Harris' Hawk (Mader 1977a) also lend importance to this investigation.

The Harris' Hawk is a species of primarily seasonally dry desert, savanna, or chaco and is here at the northern limit of its distribution; it is possible that winter conditions limit it to the north. The Red-tail, on the other hand, is here near the southern limits of its breeding distribution in arid lowlands, though it extends south into islands of the Caribbean and the highlands of western Panama (Brown and Amadon 1968).

STUDY AREA AND METHODS

I studied Red-tailed and Harris' Hawk populations from 1969 to 1976 in saguaro-palo verde (*Carnegiea gigantea-Cercidium* sp.) flatland in Pima and Pinal Counties, Arizona, where cliffs and riparian habitat are absent (Fig. 1). Details of Harris' Hawk breeding behavior and productivity, and a description of the study areas, are included in two earlier papers (Mader 1975a, 1975b) and will be referred to here only as needed for comparison with the Red-tail material.

I recorded clutch size in 59 Red-tail nests over the whole period. During the last 3 yr, when I concentrated on Red-tails rather than Harris' Hawks, I was able to determine nesting success and productivity of

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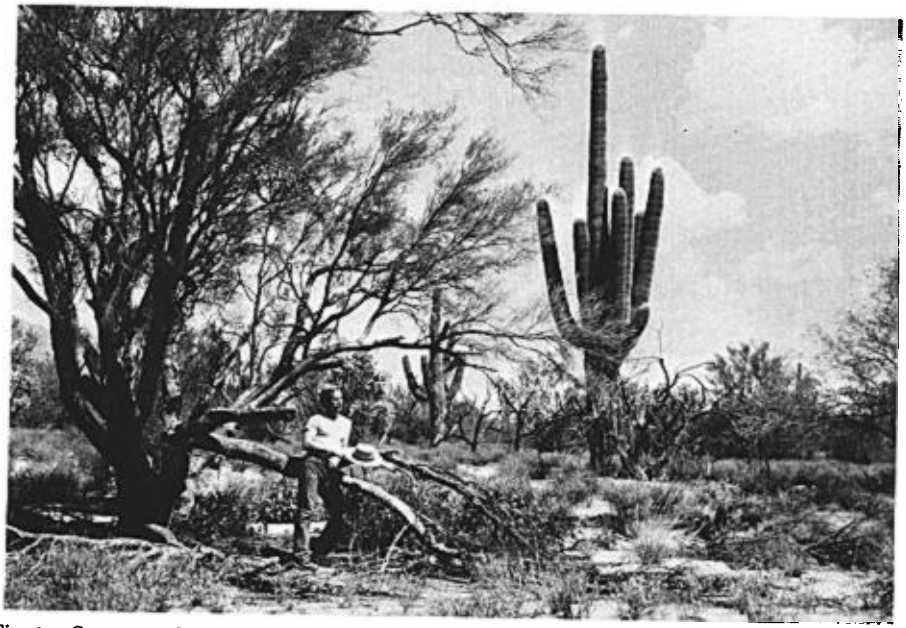

Fig. 1. Saguaro-palo verde desert in southern Arizona showing a palo verde tree on left and a saguaro on right. Triangle-bur sage (*Franseria deltoidea*) dominates the foreground.

young for 42 of these nests, and took additional notes on the ecology of the species including nest building and egg-laying dates, nest site selection, and prey remains found at nests. Red-tail and Harris' Hawk nests were located by car and on foot. Nest contents were checked periodically using an extension ladder and 1.5-m poles connected together with a mirror at the top. Nest and cactus heights were determined from these same breakdown poles to the nearest 15 cm. Approximate Harris' Hawk nest positions inside of tree canopies were measured to the nearest 5 cm from the top center of nest horizontally to nearest canopy edge and vertically to the top of the canopy. I estimated total saguaros potentially available to the hawks as nesting platforms within a nesting range (size previously determined to be about 5.0 km^2) by counting all suitable saguaros in a 0.65-km^2 area and then extrapolating these figures to 5.0 km^2.

As in my earlier Harris' Hawk study (Mader 1975a), a nest was considered successful if a chick was raised to an age of at least 28 days. Although most chick mortality occurred before 28 days, actual nest success and fledglings produced for each species may be slightly lower than figures I report here. I used a 35-day incubation period (Hardy 1939, present study) for backdating some Red-tail nests from the known hatching dates to estimated laying dates. A 46-day fledging period (Fitch et al. 1946, Johnson 1975) was used to estimate fledging dates for nests not checked late in the nesting cycle.

Two 4.8-m tower blinds were erected at two Harris' Hawk nests attended by the same three adults in 1973 (164 h) and 1974 (87 h) to determine prey species caught. A 30× scope aided identifications. The two blinds were 18.6 m and 12.2 m from the nests, respectively; both afforded clear level views of the nests.

RESULTS AND DISCUSSION

Productivity.—Some Red-tails began building nests in late December, but most appeared to build in January and February. Red-tails laid eggs from 25 February to 2 April (N = 36 nests, includes estimated dates). Overall, laying centered around the first and second weeks of March (mean = 9 March). Hatching occurred from 25 March to 8 May and centered around the first and second weeks of April (mean = 12 April). Fledging centered around the last week of May and first week of June (computed mean = 27 May). The entire breeding season (egg-laying–fledging) spanned 118 days.

TABLE 1. Red-tailed Hawk clutch size in southern Arizona

Years	Clutch size 1	2	3	4	No. eggs	No. nests	Eggs per nest
1969–1973	3	9	5	0	36	17	2.12
1974	0	7	6	1	36	14	2.57
1975	1	7	6	0	33	14	2.36
1976	1	8	5	0	32	14	2.29
Total	5	31	22	1	137	59	2.32

Red-tail nests averaged 2.32 eggs per nest (N = 59, Table 1). Harris' Hawks averaged 2.96 eggs per clutch (range = 1–4; N = 50). The clutch size distributions of the two species differed to a highly significant degree ($\chi^2 = 23.7$, 3 d.f., $P < 0.001$); 4-egg clutches were especially higher in Harris' Hawks (17, for 34%) than Red-tails (1, for 2%). Average clutch size for Red-tails in other studies has been: California, 2.00 (18 nests, Fitch et al. 1946) and 2.53 (53 nests, Wiley 1975); Utah, 2.89 (19 nests, Smith and Murphy 1973); Montana, 2.90 (22 nests, Seidensticker and Reynolds 1971); Alberta, 2.00 (98 nests, Luttich et al. 1971).

Most Red-tail nests found from 1969 to 1973 were not later checked to determine the number of young produced, hence I have such data only for the years 1974–1976 (Table 2). Of the 42 Red-tail nests, 34 (81%) were successful, producing 65 chicks (1.55 per nest attempt) of at least 28 days of age. The cause of Red-tail nesting failure was determined at only one nest. This nest, with two downy chicks, was apparently blown down by high winds. At another nest one of the adults, the female judging from size, was shot when the single chick in the nest was about 2 weeks old. The lone remaining adult raised the chick to at least 28 days of age. In Wisconsin, Orians and Kuhlman (1956) reported that 27 Red-tail nests averaged 1.80 fledglings per nest attempt in 1953, 33 nests 1.10 in 1954, and in 1955, 27 nests 1.40. Johnson (1975) estimated 1.57 fledglings per nest attempt for 121 nests in Montana, Gates (1972) 1.10 for 31 nests in Wisconsin, and Wiley (1975) 1.64 for 53 nests in California.

Henny and Wight (1972) estimated that 1.79–1.89 Red-tail young must be fledged per breeding age female in the southern United States to maintain a stable-age population. In my study 42 nests raised 1.55 chicks per nest attempt. The estimates of Henny and Wight may be slightly high for my desert study areas because nest success per year was stable and populations appeared widespread and evenly dispersed with no evidence of decline. Alternatively, it is possible that the breeding population is replenished by Red-tails coming from elsewhere.

Of the 50 Harris' Hawk nests, 34 (68%) were successful and averaged 1.60 chicks per nest attempt. Even though nest success of Harris' Hawks did not differ signifi-

TABLE 2. Red-tailed Hawk nesting success in southern Arizona

Years	N (nests)	Successful nests[a]	Chicks raised to at least 28 days	Chicks per nest
1974	14	10 (71.4%)	19	1.36
1975	14	11 (78.6%)	21	1.50
1976	14	13 (92.9%)	25	1.79
Total	42	34 (81.0%)	65	1.55

[a] A nest was considered successful if a chick was raised to an age of at least 28 days. Only nests that were initially found with eggs appear in the table. Figures in parentheses represent the number as a percentage of the total.

cantly from that of Red-tails (81%), part of the 12% difference may have been due to my investigation of the hawks in different years.

Habitat and nesting ranges.—Although I have occasionally seen Harris' Hawks in the winter in agricultural and mesquite (*Prosopis* sp.) areas, I have found them nesting only in saguaro-palo verde flatland with washes and ravines that slowly give way to low hills. When compared with adjacent steep mountains that rise abruptly out of the desert, this terrain appears relatively flat (local relief $<$100 m). Even though saguaros were sometimes locally uncommon and clearly not dominant, I still referred to the habitat as saguaro-palo verde. Red-tails, on the other hand, nested not only in flatland but in grassland, woodland, and mountainous desert outside of my study areas. On the whole, Harris' Hawks in my study areas occupied desert habitat where the vegetation was structurally complex and included saguaro, palo verde and ironwood (*Olneya tesota*) trees with assorted shrubs and cacti. Populations of small animals and birds in such areas were noticeably larger than in areas devoid of saguaros and large trees. Rabbit density in Sonoran Desert habitats is generally increased by plant species diversity through increased available edge (C. R. Hungerford pers. comm.). Also, Tomoff (1974) found that as the kinds and numbers of plants increased in the Sonoran Desert, so did the kinds and numbers of birds. In this kind of structurally complex habitat, Harris' Hawks were commonly more numerous than Red-tails and were occasionally the only large nesting hawk. In slightly less diverse desert, Harris' and Red-tailed hawks nested together. In more arid habitat, where creosotebush (*Larrea divaricata*) was the only large shrub, ironwood was absent, and saguaro and palo verde were uncommon and not of good condition and large size, Red-tails were often the only large nesting hawk encountered. On the other hand, in some seemingly good habitat, Harris' Hawks were inexplicably reduced in numbers. Harris' Hawks, then, generally appeared to occupy the most complex habitat, while Red-tails nested in simpler, more arid habitat, although some variation occurred.

Seven nesting ranges (the area and living requirements necessary for a nesting pair or trio, see Mader 1975a, Craighead and Craighead 1956: 247) of Harris' Hawks in structurally complex habitat averaged 5.0 km^2 in size. I do not have averages for Red-tail nesting ranges, but judging from the spacing at which I found Red-tail nests, I would anticipate that Red-tails occupy comparable nesting ranges in the same habitat, but much larger ones in poorer, more arid areas. Competition for nest sites seemed practically nonexistent, probably because saguaro nest sites are common. However, in one case a pair of Harris' Hawks occupied an old saguaro nest that 3 yr before had been used successfully by Red-tails. The Harris' nest was unsuccessful for unknown causes. Conversely, a pair of Red-tails occupied an old saguaro stick nest that 2 yr before was used successfully by Harris' Hawks. Outcome of the Red-tail nest was not known. I do not think that these were takeovers of nesting ranges, but a shift possibly caused when one species built a nest earlier than the other and farther away than usual from its previous site, thus allowing a neighboring species to take over the unoccupied nest.

Length of nesting cycle.—Harris' Hawks appear to have a much longer nesting season than Red-tails in saguaro-palo verde habitat. The period of egg-laying to fledging spans from February to June for Red-tails and from February to December for Harris' Hawks (Fig. 2). Time of egg-laying may vary each year. Radke and Klimosewski (1977) found a Harris' Hawk nest that fledged young from 2 to 4 December in 1975, and I have found nests with young in October. Nesting of Harris'

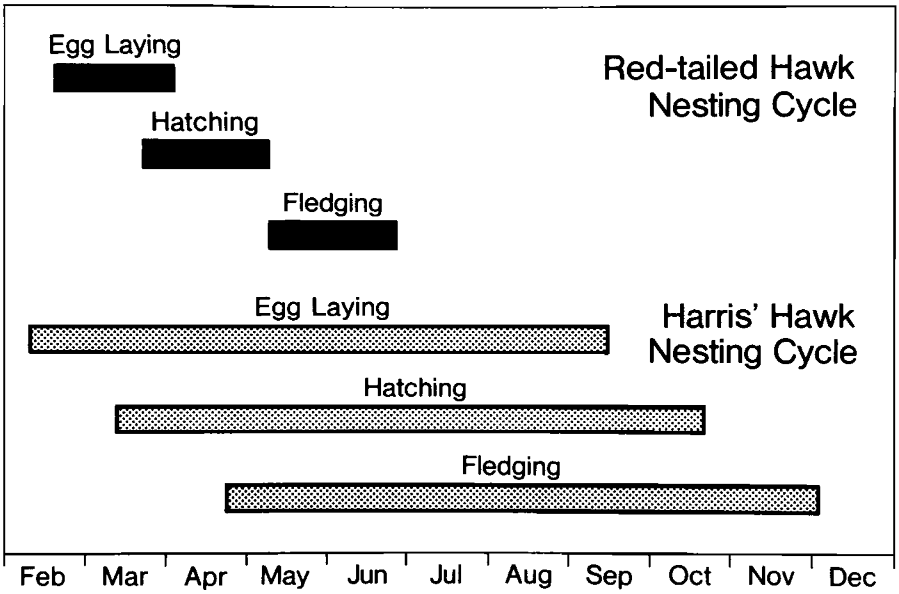

Fig. 2. The comparative duration of the nesting cycles of Red-tailed Hawks and Harris' Hawks in the Sonoran Desert of Arizona showing major events in the cycle. Second and third nesting attempts were recorded only for Harris' Hawks. Nest dates for Harris' Hawks, other than in this study, are by extrapolations of dates from Mader (1975a), and Radke and Klimosewski (1977). A 35-day incubation period was used to approximate egg-laying dates of Harris' Hawk clutches.

Hawks seemed to be centered on the period from March to June in my study years, but some pairs or trios will lay two or three clutches in one year, producing two broods (Mader 1975a, 1977b). Second nesting attempts after failure of the first appear not uncommon for Harris' Hawks in southern Arizona. However, late nesting from summer to winter may be of limited and local occurrence. To my knowledge, Red-tails have not been recorded nesting successfully twice in a year and I found no second nesting attempts. Unusually early egg-laying under optimum prey conditions or renesting by Red-tails after an initial clutch has failed may prolong the nesting season beyond that shown in Fig. 2, but apparently Red-tails do not nest in fall or winter, or if they do it is less frequent than in Harris' Hawks. Furthermore, it seems probable that Harris' Hawks may sometimes nest the year around, thereby extending the known nesting season into January, although I do not include January in Fig. 2.

Variable but sometimes extended food resources may explain why Harris' Hawks have a prolonged nesting season. Perrins (1970) indicated that food supply may limit the ability of birds to form eggs and Lack (1954, 1968) pointed out that many birds synchronize the nesting cycle to periods when food is plentiful. Thus, if eggs and young are to be produced, an adequate food supply must be on hand at the right season. My observations suggest that Harris' Hawks can sometimes breed longer and raise more broods than Red-tails for at least two reasons: (1) Habitat quality is generally better in Harris' Hawk nesting ranges, providing a longer and more continuous breeding period for important prey species and therefore a lengthened food supply, at least in certain years; and (2) Harris' Hawks are the more versatile and generalized hunter of the two and can exploit different prey types (mammals, birds, and reptiles) more effectively. The importance of each of these two factors will vary

TABLE 3. Prey types observed brought to two Harris' Hawk nests and nearby area. Both nests were attended by the same three adults

	Nest one (observed 24 March–4 May 1973)		Nest two (observed 26 July–20 August 1974)	
Prey type	No. indiv.	% indiv.	No. indiv.	% indiv.
Mammals	30	51.7	22	66.7
Birds	24	41.4	8	24.2
Reptiles	4	6.9	3	9.1
Total	58	100.0	33	100.0

because of habitat type (arid or complex), and yearly variation in climate and related changes in prey availability. For example, the reduced hunting versatility of Red-tails may be a major factor that contributes to a restricted breeding season in complex habitat, which has high densities of mammals and birds. Conversely, the hunting versatility of Harris' Hawks may be an especially important factor in low prey years if prolonged breeding is to occur.

.In support of the first hypothesis, Hungerford (1964) found that Gambel's Quail (*Lophortyx gambelii*), an important prey species of Harris' Hawks in Arizona, had a longer and more continuous breeding period when habitat quality was high, and a reduction or complete lack of breeding in drought years when habitat was poor. Two more prey species, the Cactus Wren (*Campylorhynchus brunneicapillus*) and the Mourning Dove (*Zenaida macroura*) sometimes raise two or three broods of young in saguaro-palo verde habitat (Anderson and Anderson 1973, Irby and Blankenship 1966). This and the fact that late breeding by Harris' Hawks corresponds to a late rabbit breeding peak in July and August (see Hungerford et al. 1973), suggests that in some years high quality habitat can better support a prolonged breeding season by Harris' Hawks because the required food supply is present over the necessary period of time. This rabbit peak, although available to some Red-tails, may by itself not be enough to support breeding. All the late nestings of Harris' Hawks that I observed (N = 8) were in good quality (complex) habitat. This was also true of the late Harris' Hawk nest found by Radke and Klimosewski (1977).

In support of the second hypothesis, the number of prey species and types utilized is an important indicator of hunting versatility. Previously (Mader 1975a) I identified 17 prey species from remains and prey observed brought to Harris' Hawk nests (N = 251): 6 (35%) were mammals, 8 (47%) birds, and 3 (18%) reptiles. Harris' Hawks are versatile hunters in the desert, capable of shifting prey types when availability changes. For example, I tallied prey in successive years at two Harris' Hawk nests that were attended by the same three adults, but at different times of the year, one in spring and the second in mid-summer (Table 3). The proportion of mammal prey observed brought in changed from 51.7% at nest 1 to 66.7% at nest 2, while bird prey changed from 41.4% to 24.2%. Nest 2 was the second nesting by the three hawks for that particular year and both fledged young. This trio remained together from 1973 to 1975 and in this period nested at least 6 times, producing 14 fledglings for an exceptionally high average of 4.7 per year (Mader 1977b). If nest helping is common among Harris' Hawks in southern Arizona as suggested in earlier work (Mader 1975a, 1975b), an extra adult might be advantageous by providing more food for the nestlings in late summer and fall when some prey populations have declined. Trios were present at the earliest and the two latest nestings that I recorded, and also the one observed by Radke and Klimosewski (1977).

TABLE 4. Prey remains found at Red-tailed Hawk nests in southern Arizona

Species	No. indiv.	% indiv.
Mammals		
Cottontail rabbit (*Sylvilagus audubonii*)	3	5.4
Black-tailed jackrabbit (*Lepus californicus*)	1	1.8
Unidentified rabbit	16	29.2
Round-tailed ground squirrel (*Citellus tereticaudus*)	7	12.8
Harris ground squirrel (*Ammospermophilus harrisii*)	2	3.6
Bailey's pocket mouse (*Perognathus baileyi*)	2	3.6
Southern grasshopper mouse (*Onychomys torridus*)	1	1.8
Pocket gopher (*Thomomys bottae*)	1	1.8
Wood rat (*Neotoma albigula*)[a]	1	1.8
Total mammals	34	61.8
Reptiles		
Desert spiny lizard (*Sceloporus magister*)	4	7.4
Unidentified horned lizard (*Phrynosoma* sp.)	2	3.6
Gopher snake (*Pituophis melanoleucus*)	2	3.6
Unidentified rattlesnake (*Crotalus* sp.)	1	1.8
Unidentified snakes	12	21.8
Total reptiles	21	38.2
Total	55	100.0

[a] In Mader (1975a, Tables 7 and 11) this species was misidentified as *N. lepida*.

At Red-tail nests, on the other hand, the 12 prey species from 55 prey remains included only mammals and reptiles (Table 4). The inherent bias of analyzing only prey remains data (see Snyder and Wiley 1976: 2, Mader 1975a: 70) and my modest sample size limit conclusions, but some speculation is in order. Small bird feathers at nests suggested that Red-tails preyed upon birds, but no substantial remains were found to warrant their inclusion in Table 4. At a Red-tail nest studied by Hensley (1959) in saguaro-palo verde desert, prey consisted mostly of rodents with the round-tailed ground squirrel (*Citellus tereticaudus*) most common. The desert spiny lizard (*Sceloporus magister*) and Clark's spiny lizard (*S. clarki*) were also found in this nest and an adult Red-tail was seen flying overhead carrying a snake. Snyder and Wiley (1976) showed that Red-tails preyed most heavily on mammals (50.5%) and invertebrates (36.8%) (N = 189 items from stomach analyses and prey observed caught or brought to nests). Also, prey remains found at Red-tail nests in other western states suggest that mammals are heavily preyed upon: California, 89.4% mammals (625 items, Fitch et al. 1956); Wyoming, at least 89.9% mammals (189 items, Craighead and Craighead 1956); Utah, 89.1% (330 items, Smith and Murphy 1973). In Wisconsin, however prey remains suggest that there birds are heavily preyed upon (Orians and Kuhlman 1956, Gates 1972).

Harris' Hawks are swifter and more agile in flight than Red-tails and probably better able to pursue different prey types. Harris' Hawks successfully hunted birds, mammals, and reptiles (lizards) in a variety of ways when I watched from blinds at nests (see Mader 1975a: 74). This included cooperative hunting by two or three adults. It is likely that Harris' Hawks are morphologically more adept than Red-tails at hunting in some of the close cover present in saguaro-palo verde desert, where their comparatively longer tail and slightly shorter wings are an advantage. Therefore, it seems reasonable that Red-tails in my desert areas may be more restricted feeders and less versatile hunters than Harris' Hawks, and prey primarily on mammals and to an extent reptiles.

Migratory status, duration of fledgling dependency, and behavior of the two hawk species also affect the length of the nesting season. Harris' Hawks seem largely

TABLE 5. Height of Red-tailed Hawk nests and saguaro cacti used as nesting sites

	Nest height	Saguaro height
Number nests	35	35
Mean height (m)	6.6	8.4
Range (m)	2.9–9.4	5.0–11.0

resident. Twenty-one banded Harris' Hawks (some with color bands), 13 of which were banded as chicks, were last sighted or retrapped an average of 278 days (range = 44–1,349) after their first capture at an average distance of 1,300 m (range = 400–6,800); one immature was later recovered 70 km north of its second sighting. The migratory status of Red-tails in Arizona is poorly understood. Although I banded 40 Red-tails as chicks and adults, I received only one banding return, this in the same county where I had originally captured the hawk. Young Harris' Hawks generally have an extended fledgling dependency period of at least 2–3 months, although variation occurs. I have no data on fledgling dependency of Red-tails in my study, but Johnson (1973) reports that in Montana immature birds are associated with their parents from 30 to 70 days after fledging. The long nesting period of Harris' Hawks can be attributed largely to renesting and to second broods that occur from late summer to winter. When two broods were raised in one year, the first appeared to reduce its dependency on the adults before the second clutch hatched. Even so, long dependency of fledglings on adults can occur, but this apparently does not always discourage a second brood the same year. On three occasions I saw an adult male of a trio pass prey to an immature hawk with a broken wing that was from this group's first brood of the year, even though there were chicks in a nearby nest from the second brood (see Mader 1975a: 78). This seems to be a result of the unusual social organization and behavior of this falconiform. Even if Red-tails do or could get adequate food to promote multiple clutching and brooding, the less socialized breeding structure of this species would possibly limit it.

Optimum habitat, in the form of structurally complex desert, and hunting versatility, then, may be two factors that render Harris' Hawks in saguaro-palo verde flatland less sensitive to fluctuating bird or mammal populations that might delay or prevent the food intake essential to egg-laying and a prolonged breeding season.

Snakes as possible prey.—It is not clear why Harris' Hawks do not usually prey on snakes in saguaro-palo verde desert while Red-tails regularly do so. Even though snakes, including venomous rattlesnakes (*Crotalus* sp.), were common near the Harris' Hawk nests that I studied from blinds, the hawks did not attempt to catch them, seeming to prefer comparatively lively and conspicuous mammals and birds. It is possible that Harris' Hawks react more to active prey as opposed to slower moving, less conspicuous animals such as snakes. The fact that Harris' Hawks capture fast-moving lizards with long tails that resemble snakes supports this idea. Snyder (1975) and Snyder et al. (1976) showed in laboratory settings that Red-tailed and Ferruginous (*Buteo regalis*) hawks selectively captured the more active of two prey animals. Prey activity alone does not satisfactorily explain why Harris' Hawks do not catch snakes. It may also be physically safer for Harris' Hawks to pass up snakes, if they are morphologically better adapted to capturing mammals and birds. The toes of Harris' Hawks are comparatively long and powerful for the body size (Grossman and Hamlet 1964: 280), while snake eagles typically have short, thick toes that are more suitable for gripping and killing snakes (Brown 1970: 49). As regards physical safety,

Fig. 3. An adult Harris' Hawk with young at a nest in a palo verde tree, showing type of foliage and enclosed position of nest in tree canopy. Branches immediately in front of nest have been removed.

a Red-tail was reported killed by a rattlesnake in Bent (1937). Prey activity levels and morphologic adaptation to other prey types may thus partially account for the low frequencies of Harris' Hawk predation on snakes in my study areas.

Nesting sites.—All the Red-tail nests in my study were in saguaro cacti. Nest heights of 35 nests averaged 6.6 m while heights of the saguaros used averaged 8.4 m (Table 5). Fitch et al. (1946) recorded an average height of 15.6 m for 10 nests in California, while Orians and Kuhlman (1956) observed an average height of 17.4 m for 49 nests in Wisconsin. Red-tail nests in saguaro-palo verde flatland are lower than in the above studies because saguaros are the tallest sites available.

In some saguaro-palo verde flatland, Harris' and Red-tailed hawks occupy seemingly identical habitat. In this type of habitat, where cliffs and large tree sites along riparian stream courses are absent, I found Red-tails nesting exclusively in saguaros. In comparison, Harris' Hawks nested commonly in both saguaros and trees, primarily palo verde and ironwood. Saguaro nests of both species are usually not distinguishable from one another. Harris' Hawk nests in saguaros averaged 5.9 m in height (N = 27) while total saguaro height averaged 8.2 m. These figures are about the same as Red-tail nests, and saguaro heights of 6.6 m and 8.4 m, respectively. Harris' Hawk nests in trees (palo verde and ironwood) averaged 5.7 m in height (N = 31) while total tree height averaged 7.0 m. Harris' Hawks, then, build nests at roughly the same height and utilize sites of the same height as do Red-tails, except that Red-tails use only (or at least primarily) saguaros as nesting sites while Harris' Hawks use both saguaros and trees. I hypothesize that Red-tails do not often utilize palo verde and ironwood trees in saguaro-palo verde flatland because the canopies in most of these trees are difficult to penetrate and construct nests in. Palo verde and ironwood trees are spinescent and limber. Physical injury in entering such sites may also be a factor. Twenty Harris' Hawk tree nests (12 palo verdes, 8 ironwoods) averaged 1.25 m (range = 0.50–2.85 m) horizontally from the edge of the tree canopy and 1.65 m (range = 1.10–2.35 m) vertically, indicating that large hawks, such as Harris' and Red-tails, must build nests well inside the canopy if they are to be supported (Fig. 3). Red-tails are soaring birds of usually open spaces and are not adept at regularly flying through cover. Red-tail nests in saguaros have easy access and departure routes for flight with less chance of injury. For this reason, it may not only be easier for Red-tails to utilize saguaro sites but also safer. Harris' Hawks, on the other hand, are more agile in flight and can enter saguaro and tree sites with ease.

The Great Horned Owl (*Bubo virginianus*) is somewhat agile and capable of penetrating dense cover; in saguaro-palo verde flatland it utilizes both saguaros and trees as nesting sites (Mader 1973), using old nests of course. This lends support to my idea that Red-tails nest primarily in saguaros because these sites are the most accessible platforms available and insure easy access and departure routes.

Using recorded heights of Red-tail nests as a guide and the fact that at least two saguaro limbs of sufficient size are ordinarily needed to support a nest, I estimated how many suitable nesting sites of saguaro were available for nesting Red-tailed and Harris' hawks within one nesting range (5.0 km^2). I chose a nesting range that both Red-tailed and Harris' hawks had used in the last 5 yr in "typical" saguaro-palo verde habitat. I estimated that approximately 490 saguaros were available to Red-tailed and Harris' hawks as potential nest platforms. Since Red-tails nest almost exclusively in saguaros, and but once a year, they are utilizing about 0.2% of the total platforms available for nesting in a given year. In habitat with more saguaros, the percentage is probably less, while the converse relationship may occur in habitat where saguaros are fewer. For Harris' Hawks, the percentage is probably much lower than 0.2 because so many tree sites are also available. On the other hand, if a Harris' Hawk pair or trio nests two or three times in a year, the percentage will be higher. It seems unlikely that nest site availability has any significant role in population regulation in this habitat; instead, prey densities may be an important factor.

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SOME PARAMETERS OF SONG IMPORTANT IN CONSPECIFIC RECOGNITION BY GRAY CATBIRDS

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ABSTRACT.—Some parameters of Gray Catbird song important in species recognition were identified by playback of altered song to territorial individuals. Playback types included normal song, song played backwards, song in which the order of syllables was randomized and song in which the normal frequency excursion of sound energy versus time was altered. In addition, three parameters were measured from spectrographs of songs from five individuals. Statistical analysis of the responses from 67 individuals indicated that catbirds responded to song composed of sound energy traversing an approximately 4-kHz bandwidth at a characteristic rate. *Received 20 July 1976, accepted 7 April 1977.*

THIS paper identifies some parameters of song important in species recognition by the Gray Catbird (*Dumetella carolinensis*). Catbirds are mimics and their songs are composed of imitations of other species' songs. Because of this imitative ability songs of individual catbirds are variable, and the question arises of what parameters of the song code species specificity. Previously, Thompson and Jane (1969) measured several parameters of catbird songs and Harcus (1973) examined catbird song for species distinct parameters by using playback techniques. More recently Boughey and Thompson (1976) have shown by a series of playback experiments that catbirds can discriminate their song from those of Mockingbirds (*Mimus polyglottus*) and Brown Thrashers (*Toxostoma rufum*). However, these workers were not able to identify the parameters critical for this discrimination and concluded that perhaps an average value of several parameters was important. Thompson and Jane (1969), in an investigation of the song repertoires of five individual catbirds, found that songs were composed of approximately 180 different sounds or groups of sounds. They concluded that catbirds within the same geographic region shared many of the same syllables (see Fig. 1 for a definition of terms). Harcus (1973) found random syllable sequencing and minimal syllable repetition to be important in eliciting an aggressive response from catbirds. Since Harcus' findings indicated that species information is not coded in a fixed sequence of syllable patterns of the song, some other parameters of the vocalization are suspect. The quality of catbird song syllables and syllable patterns is distinctive to the listener in the field. It thus seemed possible that catbirds might use some aspect of syllable quality as a species identification cue.

Our main investigations focused more on individual syllables and syllable patterns than on sequence analysis. We emphasized playbacks of normal and edited tapes of naturally occurring catbird syllables and syllable patterns in addition to a statistical investigation of some parameters of catbird song. We present evidence to support our conclusions that some structural aspects of syllables and syllable patterns are important in species recognition by catbirds.

METHODS

The Gray Catbird is an abundant songbird common in the forests and forest edge habitats of the northern United States and Canada. Its natural history has been described by Saunders (1935), Bent

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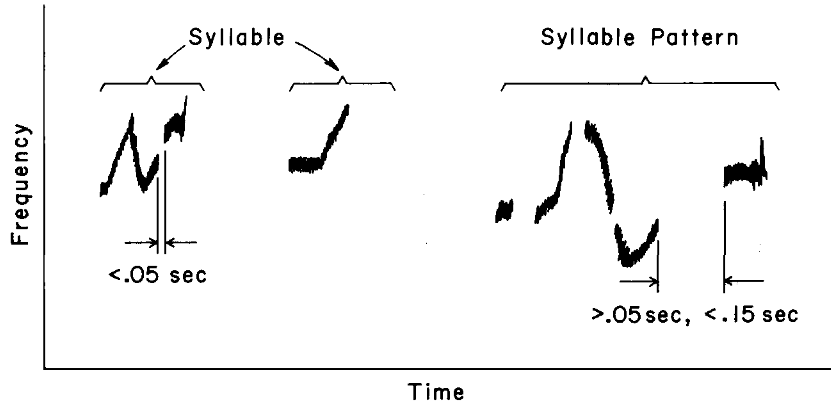

Fig. 1. Definitions of terms used in this paper. Syllables and syllable patterns are considered operationally the same. Syllables are traces on the spectrogram separated by 0.05 s or less. Syllable patterns are recurring groups of syllables separated by 0.15 s or more.

(1948), Zimmerman (1963), Darley et al. (1971) and Harcus (1973). Utilizing the fact that catbirds respond aggressively to the songs of conspecifics, playback of normal and edited tapes was used to determine some parameters of song used in conspecific discrimination. Recordings of naturally occurring song were made from individual catbirds in Old Field, New York and Nissequogue State Park in Smithtown, New York. The recordings were made at 7½″ per second on a Nagra IV-L tape recorder through a Sennheiser MD 211U microphone mounted on an 47.8-cm aluminum parabola.

Playback experiments were conducted during the 1974 catbird breeding season (May through July). Six different types of recordings composed of edited and otherwise modified portions of normal catbird song were played to 31 territorial catbirds. Individual birds were used no more than three times for playbacks. The same individual was never used twice for a playback of the same "Type." These playbacks used in 1974 are listed below and will be referred to by "Type" in the remainder of the paper (see Fig. 2).

Type 1—"Normal" is a portion of naturally occurring song recorded from a vigorously singing male in Old Field, New York. This acted as a "control" song. The response to the "control" song was used as comparison to responses to the other playback types.

Type 2—"Backwards" is the normal tape (Type 1) played backwards. This playback was designed to determine whether the syllable or syllable pattern conveyed species information even if played backwards. We predicted that "symmetrical" syllables or syllable patterns would elicit similar responses regardless of the direction in which they were played.

Type 3—"Randomized order of syllables or syllable patterns" is a tape made up of the syllable patterns from the normal tape (Type 1) but the syllable patterns along with the time intervals following them were spliced together in a randomized order according to a random number table. This playback was designed to test whether a specific sequencing of syllable or syllable pattern types was essential to elicit aggressive behavior.

Type 4—"Added randomized time" is made from the original sequence of syllables from the normal tape but time intervals of .25, .50, .75, and 1.00 s were added between the syllables or syllable patterns according to a random number table. This resulted in a playback with less sound energy per playback. This playback was designed to determine if characteristic time intervals after specific syllables or syllable patterns are important in species recognition.

Type 5—"Narrow bandwidth" is made by playing the normal tapes through a General Radio Universal Filter (Model #1932). This resulted in a tape with attenuated sound energy above 4 kHz and below 2 kHz but leaving sound energy between 2 and 4 kHz unaltered. Time intervals between syllables were affected slightly by this treatment (see discussion). Spectrographic analysis of naturally occurring catbird song indicated that the majority of syllables and syllable patterns contain energy in this 2-kHz bandwidth. We wanted to test whether energy in this 2-kHz bandwidth was sufficient to elicit aggressive responses.

Type 6—"Narrow bandwidth with added randomized time" is made from the narrow bandwidth tape (Type 5) with randomized time added in the same way and with the same time intervals as "added randomized time" (Type 4) playback.

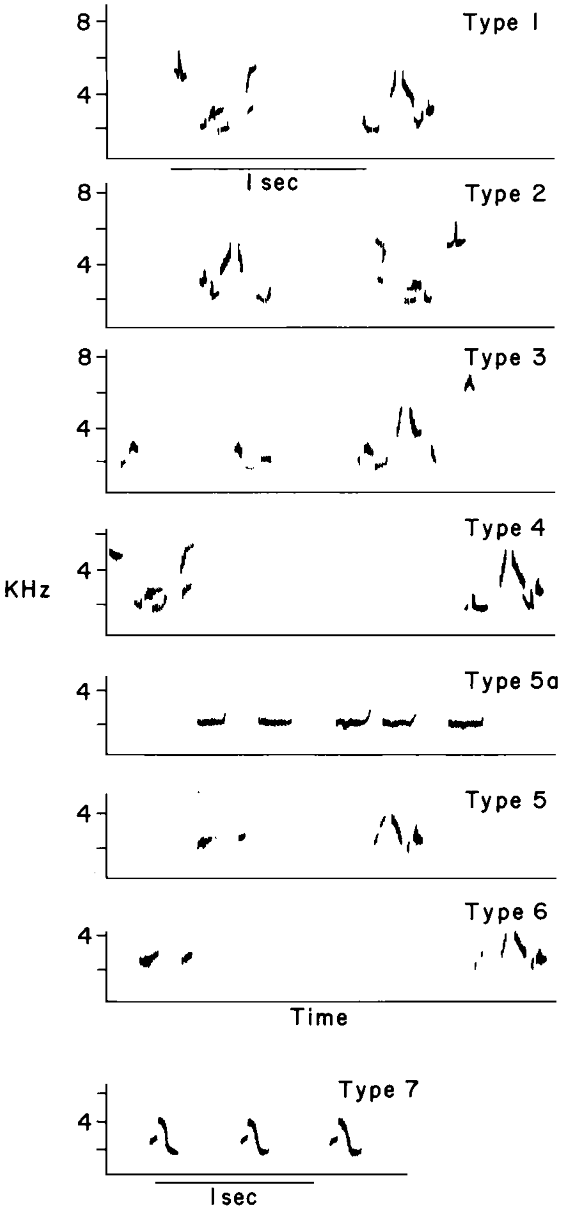

Fig. 2. Some of the syllables and syllable patterns that make up the playback loops used in these experiments. See text.

Type 7—"Wide bandwidth" excursion playback was composed of a single syllable taken from Type 1 playback. Each syllable was separated by the same time intervals as the Type 5a syllable.

During the 1975 breeding season three "Types" of recordings were used in playback experiments to 36 individuals (see Fig. 2). Each bird was used for only one playback experiment. The playback Types were:

Type 1—"Normal" which was the same playback used in 1974.

Type 5a—"Narrow bandwidth" excursion playback was composed of a single syllable taken from the Type 1 playback. This syllable subtended a narrow bandwidth and was repeated with a random order of time intervals of .12, .25, .37, .50, and .62 s. We wanted to determine whether the catbirds' response

TABLE 1. The playback type, year conducted, song length, time intervals between song, and total length of playbacks used in these experiments

	Playback type	Year conducted	Song length used (s)	Silent intervals used (s)	Total length (min)
1	Normal	1974, 1975	22, 60	22, 30	3.5, 5.5
2	Backward	1974	22	22	3.5
3	Added random time	1974	40	22	3.7
4	Random order of syllable patterns	1974	22	22	3.5
5	2–4-kHz bandwidth	1974		22	3.5
5a	Narrow frequency excursion	1975	60	30	5.5
6	2–4 kHz bandwidth with added randomized time	1974	40	22	3.7
7	Wide frequency excursion	1975	60	30	5.5

to a single narrow bandwidth syllable was stronger or weaker than their response to a single wide bandwidth syllable (Type 7).

These timings were arbitrarily selected but fall well within the normal vocalization times and intervals of silence between songs of normal catbird singing. The number of syllables composing the various playback Types were not equal. Table 1 summarizes the composition of the playback Types. In an attempt to compensate for the response differences imposed by seasonal changes, all playback types were played at least once during the beginning, middle, and late portions of the breeding season.

Sometimes during this study the various playback Types were paired with "normal" (Type 1) song. When this was done there was a 5-min silent period between playback Types. The "Normal" playback (Type 1) always followed the altered song playback. Thus Type 1 song acted as a control and was done to determine the "level of arousal" or "motivation" of the catbird at approximately the same time an altered playback Type was played. In no case was a playback of Type 1 song completely ignored. All playbacks were done using an Uher 4400 stereo recorder connected to a Nagra DH amplifier and speaker. The measured frequency response of the Uher and Nagra amplifier was adjusted to vary less than 4.0 db over the range of frequencies encountered in catbird song. The Nagra speaker was always placed 9.2 m from the Uher. We attempted to keep the volume of the playbacks consistent although physical measurements were not made. The volume of all playbacks was in the apparent range of naturally occurring catbird song. The speaker was always positioned so that a responding catbird had room to perform display flights. Catbirds live in habitats characterized by trees and bushes although there is variation in their distribution. In an effort to standardize the placement of the speaker in the habitat, it was always placed within at least 3.1 m of branches strong enough to support a catbird. Beyond this distance the branches formed a mostly continuous layer. As nearly as we could determine the speaker placement represented the behavioral center of the catbird's territory. This estimation was based on numerous observations over 2 days preceding a playback.

In 1974, 4 days were allowed between playbacks to the same bird because they apparently habituated rapidly to the playbacks. Because of this an individual bird was used only once for a playback in 1975.

A catbird's response to a playback was scored according to the scale shown in Table 2. This scale was derived from observations of natural encounters between catbirds and supported by the observations of Harcus (1973). The use of scaling assumes a number of untested judgments and the results discussed in this paper hold insofar as those judgments are correct. As the playbacks were conducted only on territories where a catbird was heard singing just prior to a playback experiment, we could be sure that the catbird was present at the beginning of the playback. The category "Response Latency" is defined as the time from the onset of the playback until the catbird comes into view and orients towards the speaker. This is the most subjective parameter of those we used. The category "Nearest Distance to the Speaker" recorded the closest approach of a bird. The category "Number and Types of Flights over the Speaker" records the two types of flights over the speaker. The swoop flight is the same as undulating flight described by Harcus (1973) and appears to represent a higher level of arousal than non-swoop flight. The "Body Postures" category records the four levels of arousal as evidenced by posture. A quivering posture with fluffed plumage and the tail down and spread is considered to indicate a high level of arousal. A bird with normal plumage contour and the tail held only slightly down but flicking is considered to be less aroused (Harcus 1973). The "Vocalization" category is divided into three levels of arousal: the soft song that appears to be the most submissive response of a highly aroused bird, the normal song that is indistinguishable from the normal maintenance song delivered by catbirds, and single syllables such as "meow" and

TABLE 2. Point scale for the responses to the playbacks

	Points
1. *Latency of response*	
a. 0–30 s	5
b. 31–60 s	4
c. 61–90 s	3
d. 91–120 s	2
e. >120 s	1
2. *Nearest distance to the speaker*	
a. 0–1.5 m	4
b. 1.51–3.1 m	3
c. 3.11–4.65 m	2
d. >4.65 m	1
3. *Number and types of flights over the speaker amplifier*	
a. each swoop flight	2
b. each non-swoop flight	1
4. *Body postures*	
a. quivering, plumage fluffed, tail down and spread	4
b. plumage fluffed, tail down and spread	3
c. plumage normal, tail down and spread	2
d. plumage normal, tail down but not spread, tail twitching	1
5. *Vocalizations*	
a. soft song	3
b. normal song	2
c. meow, grr, syllables	1

"grr" sounds that are apparently indicative of low arousal. The scores for responses to the various playback Types were compared using non-parametric multiple comparisons by Simultaneous Test Procedure (STP) or the Mann-Whitney U Test (Sokal and Rohlf 1969).

Although the main thrust if this study is the analysis of response to the playback taped in the field, the recorded songs of five different catbirds were also analyzed to determine the relatively stereotyped parameters of song common to all individuals. It seemed reasonable to assume that this might provide clues to potential species-identifying parameters. Two of these songs were recorded at the Nissequogue River State Park and three were recorded in Old Field, New York. The number of syllables and syllable patterns analyzed for each individual ranged between 294 and 332, and represented approximately 3 min of continuous song per individual. Recordings of the songs were transcribed onto a pieced-together "continuous spectrograph" made with a Kay Vibralyzer Model #7030A. A frequency range of 80–8,000 Hz with a fixed bandwidth 150-Hz filter and a 10-db dynamic range was used throughout the study. Measurements were made from the spectrographs of the duration of syllables, the interval between syllables, and the frequency limits of the syllables.

RESULTS

We attempted to determine species identifying parameters by focusing our attention on alterations of song that affected structural aspects of individual syllables and syllable patterns and the time intervals between these patterns. The responses to playbacks of these song alterations are shown in Fig. 3.

1974 playbacks.—We compared 1974 responses to various playbacks using non-parametric multiple comparisons by STP. The critical value of "U" was calculated several times for the same measurements because we were comparing unequal sample sizes. Sample sizes must be equal for this test so the number of samples of responses to playback Type 5 was reduced to 9 by random elimination of sampled responses. This reduction allows the comparison of the responses to playback Types 1, 5, and 6. Playbacks of Types 5 and 6 were sometimes followed by playback of "normal" song (Type 1) in an attempt to determine if a lack of response was due to motivational factors. Comparison of responses to Type 1 song played after Type 5

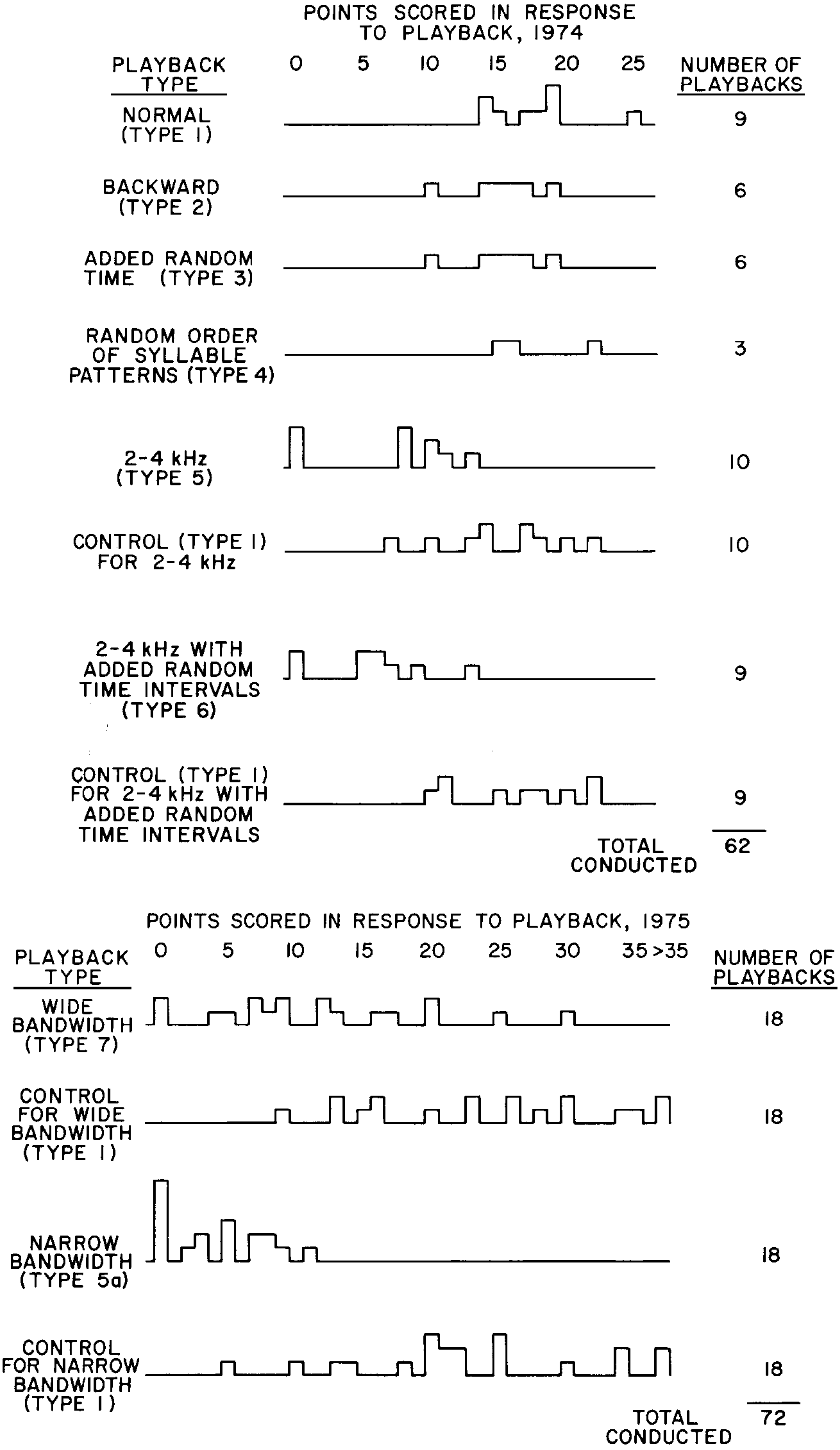

Fig. 3. The response of individuals to the playbacks for 1974 and 1975. The strength of response is plotted as histograms of the number of individuals against response score, according to the point scale shown in Table 2.

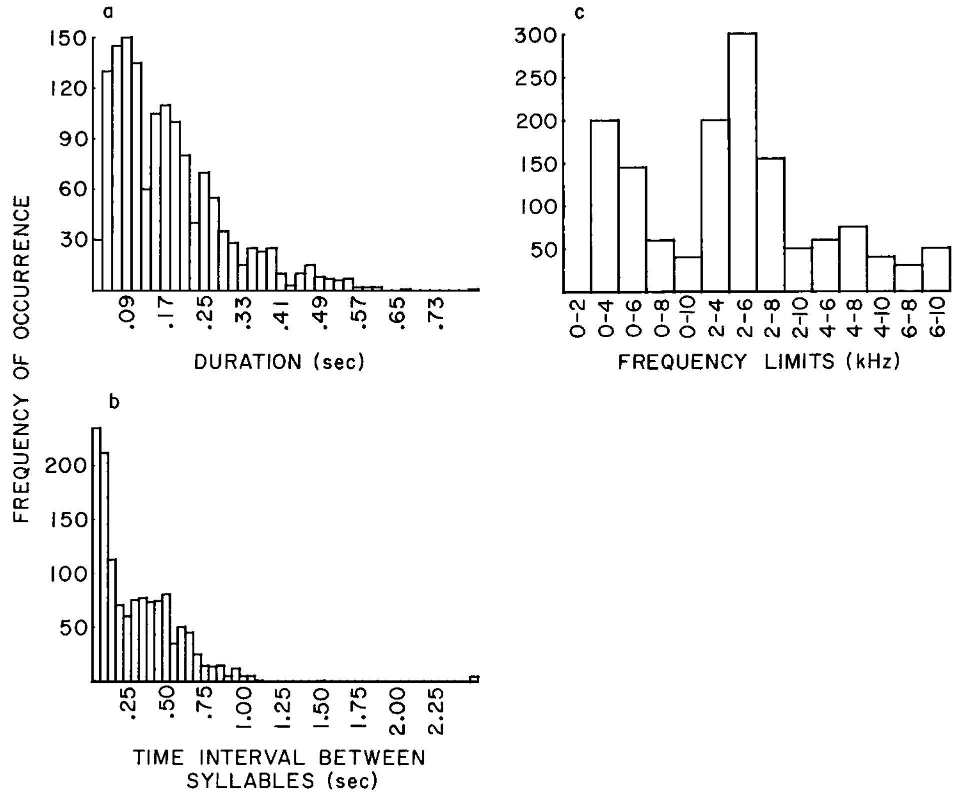

Fig. 4. Syllable patterns from combined measurements of five catbird songs: a) histogram of syllable pattern duration; b) histogram of time intervals between syllables; c) histogram of the frequency limits of five syllable patterns.

and Type 6 with responses to Type 1 song played alone showed no significant differences ($P > 0.05$). This comparison of responses was necessary to demonstrate that there was no "enhancement" or "priming effect" of playbacks 5 or 6 upon Type 1 song. However, when responses to "normal" (Type 1) playback were compared with the responses to playback of Type 5 ("narrow bandwidth") a significant difference ($P < 0.05$) was found. The catbirds responded much more strongly to "normal" (Type 1) than to Type 5 song. When the responses to the normal (Type 1) playback were compared with the responses to Type 6 ("narrow bandwidth with added randomized time") a significant difference ($P < 0.05$) was found. No significant difference ($P > 0.05$) was found in a comparison of the responses to Type 5 and Type 6 song playbacks. This indicated that "narrow bandwidth" song with naturally occurring time intervals between syllables accounted for the difference in the intensity of response to Type 1 playback compared with Type 6 playback. Responses to Type 1, Type 2 ("backwards"), and Type 4 ("added randomized time") did not differ in intensity. There were only three sampled responses to "randomized order of syllables" (Type 3) so they were not treated statistically. These three samples, however, indicated strong responses and these probably do not differ significantly from responses to the "normal" (Type 1) tape.

1975 playbacks.—The "narrow" (Type 5a) and the "wide" (Type 7) playbacks were always followed by "normal" (Type 1) playbacks so that the sample sizes (N = 18)

TABLE 3. Statistics on parameters of the songs of five individual catbirds

Individual catbirds	Duration of syllables (millis)	Time interval between syllables (millis)
Bird 1	N = 294	N = 293
	$\bar{x}$ = 147.0	$\bar{x}$ = 284.0
	SD = 112.8	SD = 213.0
	CV = 76.7	CV = 75.0
Bird 2	N = 267	N = 266
	$\bar{x}$ = 201.0	$\bar{x}$ = 337.0
	SD = 124.0	SD = 268.0
	CV = 61.7	CV = 79.5
Bird 3	N = 241	N = 239
	$\bar{x}$ = 157.0	$\bar{x}$ = 336.0
	SD = 106.0	SD = 337.0
	CV = 67.6	CV = 100.3
Bird 4	N = 332	N = 326
	$\bar{x}$ = 138.0	$\bar{x}$ = 391.0
	SD = 94.0	SD = 341.0
	CV = 68.5	CV = 87.2
Bird 5	N = 258	N = 251
	$\bar{x}$ = 138.0	$\bar{x}$ = 399.0
	SD = 94.0	SD = 406.0
	CV = 68.5	CV = 101.6

are equal. The intensity of responses by catbirds to the "narrow bandwidth excursion" (Type 5a) and "wide bandwidth excursion" (Type 7) playbacks were significantly weaker ($P < 0.05$) than the responses to "normal" (Type 1) playback. Furthermore, samples of responses to the "narrow bandwidth excursion" (Type 5a) playback differed significantly ($P < 0.05$) from "normal" playback even more than the responses to "wide bandwidth excursion" (Type 7) syllable pattern playback. Judging from the response strength, "wide" (Type 7) syllable playback is apparently more species characteristic than the "narrow" (Type 5a) syllable pattern playback, although both syllable types normally occur in catbird song.

Statistical analysis of naturally occurring song.—Sample population variability of three parameters of song for five individuals is shown in Fig. 4. The mean, standard deviation, and coefficient of variation were calculated for the duration of syllables and the interval between syllables for each of five catbirds (Table 3). Eleven intervals were extemely hard to measure accurately and were eliminated from analysis. The results showed that durations of syllables and syllable patterns and the intervals between syllables and syllable patterns did not differ between individuals. These findings suggested that there was no dependence of time interval occurring after or before a syllable (or syllable pattern) of a particular duration. An R × C Test of independence showed that there was no dependence of one parameter on the others. Only the frequency limits of the syllable (or syllable pattern) and the duration of the syllable (or syllable pattern) showed dependence. In other words, the difference between the highest and lowest frequency excursion of a syllable predicts the length of that syllable. Most syllables had a characteristic frequency excursion of 4 kHz.

DISCUSSION

Our playback experiments and the descriptive analysis of the catbird song revealed several parameters that appear to be important in conspecific recognition by catbirds. One important parameter is the frequency excursion or sweep of normally occurring syllables. Harcus (1973) found, and our results confirm (Playback Type 3), that a second important characteristic of song for species recognition is a lack of monotony (high syllable diversity) in the syllable patterns.

The response of the catbirds to the "backwards" (Type 2) and "added randomized time" (Type 4) playbacks did not differ significantly from the responses to the "normal" (Type 1) playbacks. These results are in agreement with Harcus' (1973) findings that changes in the gross temporal organization of the song had little effect on the elicited aggressive response of the catbird. He noted too that in the wild, individual catbirds often vary the temporal arrangement of their song from discontinuous to continuous. The catbird's similarly strong response to songs played forward or backward may be explained in at least two ways. Some structural aspect (e.g. harmonics) of the syllables and syllable patterns may be important rather than their specific morphology. If the morphology of the syllable is important, one would predict that the symmetrical shape of many of the syllables should result in it making little difference in how they sound when they are played forward or backward. It is not possible from our results to tell whether quality or morphology is most important.

Thompson and Jane (1969) concluded from their analysis that there is no fixed order of syllables or syllable patterns in catbird song. We tested this parameter but since there were only three playbacks in which the order of the syllables was randomized (Type 3) they were not treated statistically. The responses to Type 3 are strong, however, and imply that the catbirds do not discriminate them from "normal" (Type 1) playbacks. Other bird species apparently ignore sequence information (Bremond 1968, Emlen 1972). Because the specific order of syllables or syllable patterns, the temporal organization, or the direction in which syllables were played did not appear to be crucial in species recognition by catbirds, we altered song in ways that affected the tonal quality of the syllables. These included Types 5, 5a, 6, and 7. However, several problems existed with the 1974 playbacks that used frequency filtering. When a frequency filter is used to filter a normal song, the duration of some syllables is decreased, and the interval between these syllables is increased. Sound energy falling outside of the 2–4-kHz bandwidth is strongly attenuated, and if the energy that begins or ends a syllable is attenuated, then the syllable length and the interval associated with it are altered. This means that several parameters will co-vary, making interpretation of the results even more difficult. Because of these considerations, different kinds of bandwidth excursion playbacks were used in 1975. The significantly stronger response of the catbirds to the "normal" (Type 1) playback than to Types 7 or 5a indicates that some parameter of the song other than the bandwidth excursion is also important. That parameter is almost surely the increased variety of syllables and syllable patterns characteristic of the Type 1 playback. It is important to note that Types 5, 5a, and 7 are all significantly poorer in eliciting measured responses from catbirds. When compared to Type 5a, Type 7 elicits a significantly stronger response.

In general, the responses to the normal playbacks in 1975 were stronger than to the 1974 normal playbacks. We believe that this is most likely due to the change in procedure in 1975. In the 1974 playbacks we found that when a bird was used more than once its response declined, regardless of what type of playback was used. Therefore, during the spring and summer of 1975 each bird was used for only one set of playbacks. The playbacks used during 1975 are also 2 min longer, providing more response time.

Besides doing playback experiments in the field, normal catbird song recordings were analyzed. Measurements of naturally occurring song show that all measured parameters are highly variable and therefore unlikely to be used as cues in conspecific recognition. It is interesting to note that we found essentially the same mean duration of syllables as those reported by Thompson and Jane (1969).

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NOMENCLATURE OF THE BLACK-BELLIED WHISTLING-DUCK

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Abstract.—There are two distinguishable subspecies of the Black-bellied Whistling-Duck, one in South America to eastern Panama and one from western Panama through Central America to the southernmost United States. The type locality of the species is the West Indies, but there is little evidence that birds from that area are anything but vagrants or birds imported from South America. All records of this species in the West Indies are attributable to the subspecies that occurs naturally in South America. The plate and description on which the name of the species is based seem to be of the South American form.

It thus becomes clear that the South American and West Indian populations of Black-bellied Whistling-Duck must bear the name *Dendrocygna autumnalis autumnalis* (Linnaeus) 1758 and that *Dendrocygna discolor* Sclater and Salvin 1873 is a junior synonym. The earliest available name for the birds north of Panama is *D. a. fulgens* Friedmann 1947, of which *D. a. lucida* Friedmann 1947 is a synonym. *Received 10 November 1976, accepted 16 April 1977.*

The specific name for the Black-bellied Whistling-Duck, *Dendrocygna autumnalis* (Linnaeus 1758), was based on a plate and description published in 1751 by Edwards, who stated that the bird he saw had come from the West Indies. More than a century later, Sclater and Salvin (1873) described *Dendrocygna discolor*, applying the name to birds of "Venezuela, Guiana, and Brasilia." In later treatments where South American birds were listed as the race *discolor* of the species *D. autumnalis*, the Central and North American populations as well as birds of the West Indies were allotted to the nominate race. This concept of two subspecies, divided by an apparently natural distributional gap in Panama (Wetmore 1965) was long accepted.

Todd and Carriker (1922:140) called attention to variability in the South American population, noting that birds from the Santa Marta region of Colombia were more rufescent on the breast than some specimens from eastern Venezuela. Friedmann (1947) examined a specimen from Puerto Rico and studied Edwards' (1751) plate and description, and concluded that both were similar to birds from western Venezuela, northern Colombia, and eastern Panama, all of which he considered to represent nominate *autumnalis*. Friedmann thus restricted *discolor* to the more eastern and southerly portions of the South American range of the species. At the same time, Friedmann provided two subspecific names for the Central and Northern American Black-bellied Whistling-Ducks, *fulgens* for birds of southern Texas and northeastern Mexico and *lucida* for those in the remainder of Mexico and Central America to western Panama, thus admitting four races of the species.

Hellmayr and Conover (1948:314–315) disagreed with Friedmann's (1947) analysis, reidentifying Friedmann's Puerto Rican specimen and three others from the West Indies (Puerto Rico and St. Vincent) as *discolor* and considering the birds from northwestern South America to be intermediate between South and Central American populations but assigning them to *discolor*. They considered Edwards' plate representative of the North and Central American populations, which thus retained the name *autumnalis*, and rejected both of Friedmann's newly proposed names as being based on variation due to age and freshness of plumage.

Each of the taxonomic concepts set out above attracted followers in the three subsequent decades. Delacour (1954), Rylander and Bolen (1970), Meyer de Schauensee (1964) and others have followed Hellmayr and Conover (1948) in recognizing two races of this species. On the other hand, Friedmann's concept of four subspecies has been accepted in the Mexican check-list (Friedmann, Griscom and Moore 1950) and by Blake (1953), among others. Still a third concept, which might be called "modified Friedmann," has developed, accepting Friedmann's (1947) disposition of the names *discolor* and *autumnalis* but utilizing only the name *fulgens* for the populations north of Panama. This course, suggested by Pitelka (1948), has been followed by the A.O.U. check-list (1957) and by Wetmore (1965). Thus, one presently has good authority for recognizing two, three, or four subspecies of *Dendrocygna autumnalis*.

The problem can be broken down into three questions. First, are there one or two distinguishable populations in South America? Second, are there one or two distinguishable populations in Central and North America? Third, with which (if any) of these populations do birds of the West Indies, and particularly the one figured by Edwards, agree?

South American birds.—I see no essential difference among birds from various parts of South America in the collection of the National Museum of Natural History (USNM). In none of them is the neck concolorous with the back, as it is in Central and North American birds. In all of them the reddish of the back of the neck is separated from the chestnut of the back by a collar or cape of gray or of paler brown. Both the brown and gray collars occur in birds from Paraguay and those from Colombia and eastern Panama, and, as Hellmayr and Conover (1948) suggest, this variation may be related to age or plumage condition. The make of the skin, particularly the degree to which the neck is telescoped or stretched, may account for part of the variability. Birds from Colombia and Panama tend to have browner capes than those from Brazil and Paraguay, although individuals from the two geographic extremes can be matched almost exactly in this respect. Two Venezuelan specimens have the purest gray capes.

The comparison is essentially the same ventrally. In all South American birds examined there is a rather broad intervention of gray or grayish brown between the rufous of the breast and the black of the abdomen. This area is more frequently brownish gray in birds from Colombia and Panama, but again extremes from those countries can be matched by individuals from Brazil and Paraguay. Ventral coloration in general seems to be subject to staining that masks or modifies the true color.

Although there is considerable variation in the series of 25 South American (including eastern Panama) birds examined, it seems not to be geographically oriented, nor is it comparable to the degree of difference between South America populations and those of Central and North America. I conclude that there is but one recognizable South American form of this whistling-duck, agreeing with Hellmayr and Conover (1948).

Central and North American birds.—I can distinguish no significant geographic variation in dorsal color in a series of 15 birds of the Central and North American population, available specimens of which range from Texas to Costa Rica. In all birds the lower neck is concolorous with the back, with none of the interrupting gray and grayish brown found in the South American birds. The rather small amount of variation in the shade of rufous of the back is not geographically correlated.

There is more color variation ventrally than dorsally in these birds, but again I detect no geographic correlation. In some individuals there is a narrow band of grayish- or yellowish-brown between the rufous or chestnut breast and the black abdomen, but this is never as extensive as in South American birds. This narrow band of lighter color occurs only on those birds with paler breasts, supporting the suggestions of Hellmayr and Conover (1948) and Pitelka (1948) that Friedmann's (1947) separation of *lucida* from *fulgens* was based on characters related to age or plumage condition. I conclude that the Central and North American population cannot be divided racially, again agreeing with Hellmayr and Conover (1948).

Birds from the West Indies.—Friedmann (1947) and Hellmayr and Conover (1948) agreed that a specimen from Añasco, Puerto Rico, is similar to South American rather than Central American birds, although they differed in their nomenclatural interpretation of this identification because of differing concepts of variation in South America. I agree with them in assigning that bird to the South American subspecies as defined here. Hellmayr and Conover (1948) also assigned another Puerto Rican specimen and two from St. Vincent to the South American form. Bond (1952) reported other West Indian specimens as being of the South American form, and indeed all specimen material of *D. autumnalis* from the West Indies has been so identified.

Identity and origin of the type.—Friedmann (1947) identified the bird in Edwards' (1751) plate, upon which the Linnaean name is based, as the South American form because of the separation of the red breast from the black belly by an area of "dusky ash colour" mentioned in Edwards' text and which is apparent to some extent in the plate. In this character I agree with Friedmann (1947) that the figured bird resembles South American birds. (The plate in the 1803 edition of Edwards' work, published by Will Gardner, London, is of no value in identifying the race of the subject bird.) The 1751 plate does not show, nor does Edwards' text mention, a grayish or grayish brown cape separating the reddish of the neck from the red back. In the continuity of color from the neck to the back the bird in the plate resembles Central American birds.

Hellmayr and Conover (1948) remarked that although some specimens from the population of northwestern South America "could be said to agree with Edwards' description and plate, so do others" from the Central and North American population. They noted that in the latter birds "at the junction with the black belly the under parts are buffy grayish, this color gradually shading into the dull reddish of the upper breast. We take these specimens to be young birds not yet in full plumage." The northern birds in USNM that possess this narrow light band at that junction do not have fully black thighs, probably another sign of their immaturity. By contrast, the South American birds do retain the ashy breast patch after they have acquired black thighs. The blackness of the thighs is a character mentioned and figured by Edwards (1751) and specifically noted by Hellmayr and Conover (1948) and Friedmann (1947).

Only one other character mentioned by Edwards (1751) has a potential for indicating which population was represented by the bird he saw; this is the color of the lesser upper wing coverts. Edwards states: ". . . next above the White is a Plat of bright Orange-Colour . . . ." The figure shows an exaggeratedly large and bright orange wing patch. In none of the birds available are these coverts so prominent or distinctively colored. They are, however, slightly brighter and contrast more with the back color in South American than in Central or North American birds.

Considering that Edwards was not attempting to illustrate subspecific differences when he prepared his plate, it is not surprising that any identification of the bird at that level must be somewhat speculative. On the basis of the combination of the ashy gray breast patch and black thighs, and because of the relative distinctiveness of the "orange" wing patch, and despite the lack of a grayish cape, I conclude that the bird figured is more similar to those of South America than to Central or North American birds. This finding agrees with the view of Friedmann (1947).

Some additional evidence may be brought to bear on the identity of the bird Edwards saw, relative to its origin in the West Indies. Friedmann (1947) suggested that "It is quite possible that the bird described by Edwards did not really come from there at all." However, Edwards figured many birds and mammals from the West Indies in his natural history series, and comments scattered through the 1751 volume suggest that there was a rather brisk importation of wildlife from the West Indies to Europe at that time. Bond (1950) suggested that the bird may have come from Jamaica, citing in support March's (1864) report that this species was imported into Jamaica from the Spanish Main, that is, the north coast of South America.

Gosse (1847) reported that although the species *D. autumnalis* was much less common in Jamaica than *D. arborea*, it was found there in some seasons, as an autumnal visitant from the Spanish Main. Gosse saw some that had been imported to Jamaica. March (1864) reported that *autumnalis* was sometimes met with in some of the eastern parishes of Jamaica, but he never saw any other than birds imported into Kingston from the Spanish Main. Both these accounts predate the naming of the South American birds, so no subspecific inference should be drawn from the use of the name *autumnalis* rather than *discolor*. Cory (1889) called *D. autumnalis* accidental in Jamaica and did not mention either *autumnalis* or *discolor* on any other island.

A number of old records for Puerto Rico give varying accounts of status and numbers of *D. autumnalis*. Taylor (1864) considered the species abundant and a breeding bird. Wetmore (1916) reported it as formerly abundant but becoming rare. Struthers (1923) reported collecting eggs and young. Danforth (1926) stated that it was not uncommon in autumn but rarely nested. However, Wetmore (1927), noting that his own earlier report was in error, cited all the above records in the synonymy of *Dendrocygna arborea*, and did not mention *D. autumnalis* as a Puerto Rican species. More recent accounts of Puerto Rican birds (Bond 1961, Leopold 1963) regard *D. autumnalis* as a vagrant or accidental species there, although Biaggi (1970) uncritically accepts the older published records.

Bond (1950, 1952) considered the South American form casual in West Indian islands north of Trinidad, and did not mention records of the northern race. More recently Bond (1961) discussed "The South American race (*D. a. discolor*) which is found in the West Indies . . ." and stated that this form was "apparently vagrant from South America." There is little evidence that Black-bellied Whistling-Ducks ever occured in large numbers in the West Indies, or that they ever occurred there except as stragglers or imports from South America. There is no evidence that birds of the Central and North American race ever occurred there.

The South American and West Indian populations of Black-bellied Whistling-Duck must thus bear the name *Dendrocygna autumnalis autumnalis* (Linnaeus) 1758. *Dendrocygna discolor* Sclater and Salvin 1873 is a junior synonym. The earliest available name for the birds north of Panama is *D. a. fulgens* Friedmann 1947, of which *D. a. lucida* Friedmann 1947 is a synonym.

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FACTORS AFFECTING NESTING SUCCESS OF THE GLOSSY IBIS

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ABSTRACT.—We studied Glossy Ibis nesting success in New York during 1974 and New Jersey during 1975. The clutch size in New York (2.56) was significantly smaller than in New Jersey (2.93). Fewer eggs hatched in New York, due to higher rates of predation, nest abandonment, and perhaps egg infertility. Including only nests in which at least one egg hatched, however, the same number of eggs hatched in New York and New Jersey, but significantly fewer chicks fledged in New York. The third egg in a nest hatched at a significantly longer interval from the first egg in New York than in New Jersey. In New York, no third chicks fledged, while in New Jersey 37% fledged. Starvation and predation on all chicks were highest in New York. The daily weight of chicks up to 10 days of age was significantly lower on most days in New York, but the rate or length of feeding bouts did not differ from that in New Jersey. This suggests a lower food supply in New York, which may explain the lower clutch size, greater hatching asynchrony, and greater chick starvation in New York, but colder temperatures and rainfall on more days in New York undoubtedly also contributed. Feeding behavior appears not to be as adjustable to prevailing conditions as clutch size and asynchronous hatching. *Received 14 September 1976, accepted 3 July 1977.*

THE northward expansion of the breeding range of the Glossy Ibis (*Plegadis falcinellus*) from Florida since 1940 is well documented (Steward 1957, Hailman 1959, Bull 1974). Factors such as colony and nest site selection (Burger and Miller 1977) and colony success should be examined to help understand this rapid expansion. There are no detailed studies of the nesting success of the Glossy Ibis in North America. The success of some Ardeids that nest with ibises, however, has been investigated (e.g. Meanley 1955; Teal 1965; Dusi and Dusi 1968, 1970; Jenni 1969; Pratt 1970, 1972; Taylor and Michael 1971). Except for Pratt's studies, these authors studied nesting success during only one breeding season in only one area. Yet for many avian species, success varies between years and sites (see Klomp 1970). In this study, we compare the nesting success of the Glossy Ibis in two mixed colonies in New York during 1974 with that in two mixed colonies in New Jersey in 1975. Ibises have been breeding near Brigantine, New Jersey since 1957 (Potter and Murray 1957), which was their northern breeding limit until 1961, when they began breeding on Long Island, New York (Post 1962). In 1973 they began breeding in Maine (Finch 1973). We were especially interested in the overall success of the colonies and in the nature, timing, and causes of nesting failure as possible contributing factors to the northward expansion of Glossy Ibis.

STUDY AREAS AND METHODS

The four colonies studied were similar with respect to vegetation and nest placement. The predominant vegetation was common reedgrass *Phragmites australis*, bayberry *Myrica pennsylvanica*, and poison ivy *Rhus toxicodendron*. All ibis nests were on the ground, except for the reuse of several nests of Snowy Egrets *Egretta thula* in New York (Burger and Miller 1977).

The two New York colonies were in Jones Beach State Park on Long Island, New York. The Meadowbrook colony, behind parking field #1, contained 113 nesting pairs: 71 pairs of Glossy Ibis and 42 pairs of Black-crowned Night Herons (*Nycticorax nycticorax*). The Loop colony, 3.2 km northwest of Meadow-

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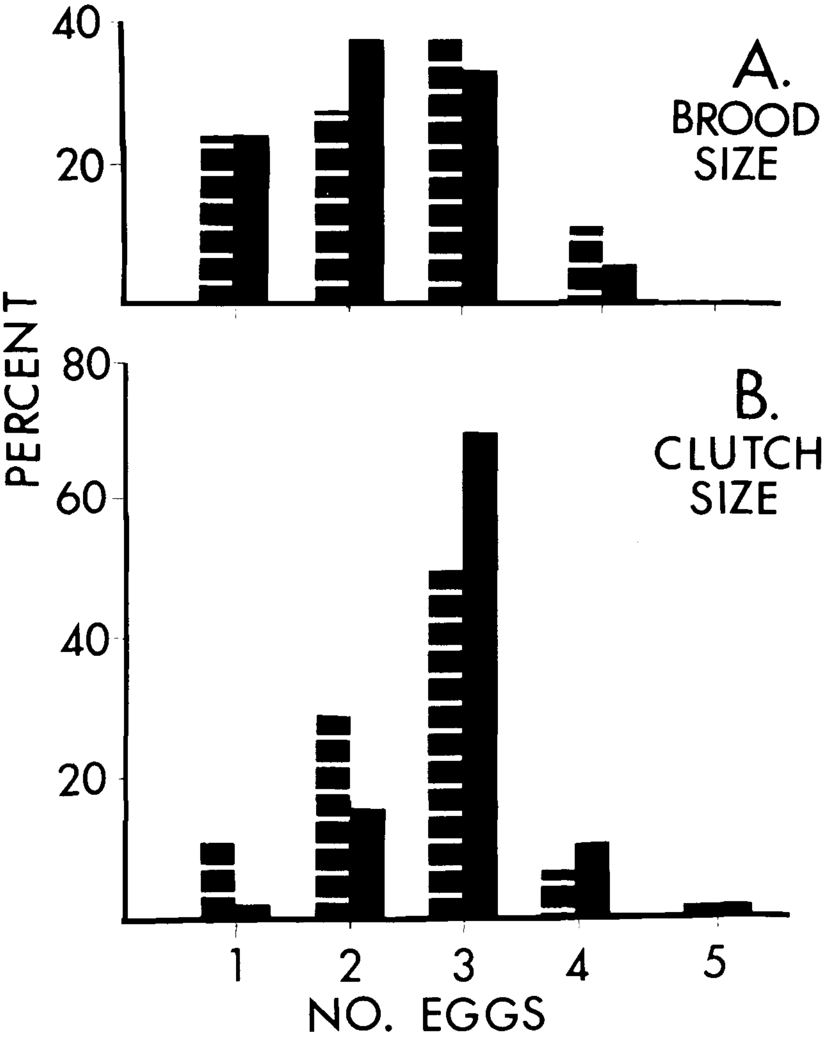

Fig. 1. Brood and clutch size of Glossy Ibis as a function of locality. New York = broken bar; New Jersey = solid bar. **A.** N.Y., N = 37 nests; N.J., N = 58 nests. **B.** N.Y., N = 95 nests; N.J., N = 76 nests.

brook, off the Loop Parkway, contained 152 pairs: 64 pairs of Glossy Ibis, 12 pairs of Black-crowned Night Herons, and 76 pairs of Snowy Egrets. Two hundred to 250 pairs of Herring Gulls (*Larus argentatus*) nested on the open sand and beach grass surrounding each colony.

The two New Jersey colonies studied were each located on a small island in Absecon Bay, north of Atlantic City. Island I (at channel marker 71) contained 1,225 nesting pairs: 300 pairs of Glossy Ibis, 335 pairs of Snowy Egrets, 330 pairs of Little Blue Herons (*Florida caerulea*), 125 pairs of Louisiana Herons (*Hydranassa tricolor*), 25 pairs of Great Egrets (*Casmerodius albus*), and 60 pairs of Cattle Egrets (*Bubulcus ibis*). Island II (at channel marker 61) contained 800 nesting pairs: 175 pairs of Glossy Ibis, 80 pairs of Black-crowned Night Herons, 200 pairs of Snowy Egrets, 208 pairs of Little Blue Herons, 65 pairs of Louisiana Herons, 48 pairs of Great Egrets, and 24 pairs of Cattle Egrets. Sixty to 120 pairs of Herring Gulls nested in *Spartina* around each colony.

Data were collected from mid-April through early August in 1974 and from mid-April through late June in 1975. To determine nesting success, 95 nests in New York (57 at Meadowbrook and 35 at the Loop) and 76 in New Jersey (31 on Island I and 45 on Island II) were followed from egg-laying through 25 days after hatching. Nests were sampled from at least two different areas within each colony. Study sites were

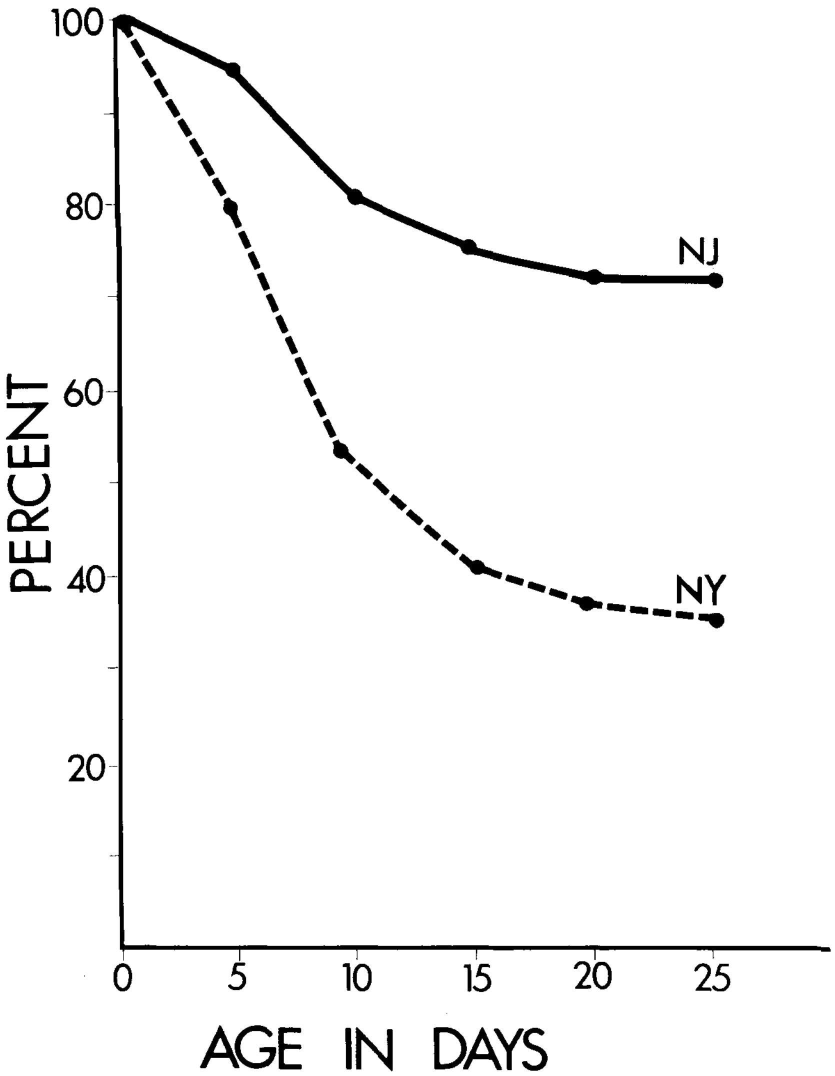

Fig. 2. Survival of Glossy Ibis chicks with age as a function of locality. N.Y., N = 87 chicks from 37 nests; N.J., N = 112 chicks from 58 nests.

sufficiently far apart so that only birds from the area being censused would flush. Adults incubated all sample nests for at least 3 days. Nests were checked every 2–4 days during incubation and every 1–2 days after hatching. The area around the nests was searched for preyed upon eggs and dead chicks. Temperature and precipitation data were taken from monthly reports issued by the National Oceanic and Atmospheric Administration.

Young chicks were marked with a small spot of acrylic paint on the head, and chicks older than 10 days were banded with U.S. Fish and Wildlife Service aluminum bands and color bands. Chicks up to 14 days of age were weighed to the nearest 1.0 g on Pesola field scales. Chicks 11–15 days old leave the nest when approached, but they can be identified by the color bands since they remain within about 7 m. Chicks older than 15 days, which spend increasingly less time at the nest, were censused by observations from a small portable blind. Chicks older than 25 days could not be adequately censused.

Since human disturbance is known to cause some nesting failure in Cattle Egret colonies (Blaker 1969), we minimized disturbance by checking nests rapidly and quietly, checking only in the morning when temperatures were lowest, and not checking during heavy rain. By sampling nests in several widely

TABLE 1. Glossy Ibis success differences in New York and New Jersey for (A) all original sample nests and (B) only nests in which at least one egg hatched. Means, the 95% confidence limit (under each mean), and the tests of significance are based on square root transformations of the raw data ($X' = \sqrt{X + 0.5}$)

	N	$\bar{X}$ Eggs laid/nest	$\bar{X}$ Eggs hatch/nest	$\bar{X}$ Chicks fledge/nest
A. All nests				
New York	95	2.56 (2.49–2.63)	0.67 (0.45–0.89)	0.43 (0.16–0.73)
New Jersey	76	2.93 (2.78–3.07)	1.46 (1.19–1.75)	1.09 (0.62–1.63)
Test of significance		t = 4.54; $P < .001$	t = 4.40; $P < .001$	t = 5.22; $P < .001$
B. Viable nests				
New York	37		2.26 (2.22–2.59)	0.85 (0.46–1.30)
New Jersey	58		2.13 (1.93–2.32)	1.28 (1.04–1.72)
Test of significance			t = 0.70; N.S.	t = 3.72; $P < .001$

separated areas, adults were kept off the nest only a short time. Since the amounts of disturbance in New Jersey and New York were equal, we assume its effect on success was similar.

RESULTS

Egg-laying.—In New York, egg-laying extended for 23 days at Meadowbrook (8–30 May 1974) and for 37 days at the Loop (13 May–18 June 1974). The ibises laid later than other species in the colony. At Meadowbrook the first ibis egg was laid 20 days after the first Black-crowned Night Heron egg. At the Loop, Black-crowned Night Herons and Snowy Egrets began laying at least 12 days earlier than ibises.

In New Jersey, egg-laying extended for 21 days on Island II (1–24 May 1975) and for 24 days at Island I (6–29 May 1975). All species initiated laying within 5 days of each other.

Clutch size and overall success did not differ significantly between the two colonies in each state, so the means were pooled for each state. One to 5 eggs were laid per nest. The most frequent clutch was 3 in both states (Fig. 1).

The mean clutch size in New York (2.56) was significantly smaller than the mean clutch in New Jersey (2.93) (Table 1A). These clutch sizes are within reported ranges: 2.93 in Virginia (Williams 1975); 2.62 in New York (Bull 1974); 1–5 in Europe (Ali and Ripley 1968); 1–3 in Georgia (Shanholtzer 1970).

Egg survival.—In New York, 64% of all eggs (N = 243) never hatched whereas 44% of all eggs (N = 225) never hatched in New Jersey. The greatest egg loss was to predators: 41% in New York and 33% in New Jersey. An egg was considered preyed upon if it was punctured and its contents at least partly eaten, or if it disappeared.

Predators in both areas were Herring Gulls, Fish Crows (*Corvus ossifragus*), and possibly Norway Rats (*Rattus norvegicus*) and Black-crowned Night Herons. Herring Gulls nested in large numbers on the periphery of all colonies. Once we saw a gull land near an incubated nest, causing the ibis to fly, and the gull removed one egg. Four partly-eaten ibis chicks were discovered near gull nests. At least one pair of crows nested within each colony. They were frequently observed entering the colony. Norway Rats were seen and Black-crowned Night Herons nested in all colonies, but their effect is unknown.

It was difficult to determine other causes of egg loss; infertile, abandoned, cracked,

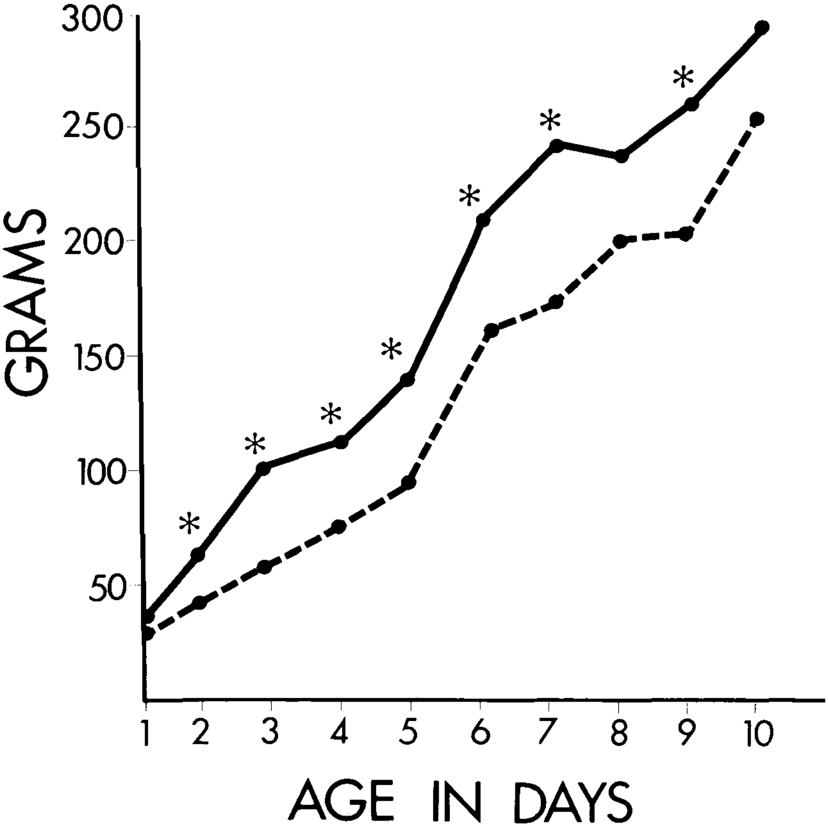

Fig. 3. Weight of Glossy Ibis chicks as a function of locality. New York = broken line (N = 29 chicks); New Jersey = solid line (N = 21 chicks). Differences between states are statistically significant ($P < .05$; based on t-test) for starred days.

or eggs found outside of nests accounted for 23% of all eggs in New York and 11% in New Jersey.

Egg hatching.—Thirty-six percent of all eggs hatched in New York and 56% hatched in New Jersey. Including all original nests, significantly fewer eggs hatched per nest in New York compared to New Jersey (Table 1A). However, including nests in which at least one egg hatched ("viable nests"), the same number of eggs hatched in New York and New Jersey (Table 1B).

In both states, the second chick hatched about 1 day after the first chick. The third chick in New York, however, hatched at a significantly longer interval from the first chick than in New Jersey (Table 2). In both states, incubation began after the first egg was laid, so delayed hatching reflected delayed laying. In New York, the mean

TABLE 2. Hatching interval ($\bar{X}$ ± 1 SD days) for Glossary Ibis chicks in New York and New Jersey when the initial brood size was three

	1st–2nd Chick	1st–3rd Chick
New York	1.1 ± 0.79	4.3 ± 2.53
New Jersey	1.1 ± 0.87	2.3 ± 0.85
Test of significance	t = 0.31, d.f. = 55, N.S.	t = 2.69, d.f. = 31, $P < .01$

temperature (at a station 18 km NW) during egg-laying was 15.5°C, which was 1.06°C below normal for that period, and 9.7 cm of rain fell. During egg-laying in New Jersey, the mean temperature (at a station 7 km SW) was 16.3°C, and only 6.8 cm of rain fell.

Chick survival.—The greatest period of chick loss was between hatching and 10 days of age (Fig. 2). In New York only 52% of the chicks survived to 10 days and 36% survived until day 25 ("fledging"). In New Jersey, 80% survived to 10 days and 71% survived until day 25.

Weights of chicks up to 10 days of age were taken daily in all colonies. There were no significant differences in weights on any day for the two colonies in each state, so the data were pooled. Comparably-aged chicks weighed significantly more in New Jersey than in New York on most days (Fig. 3). Differences in weights could be due to differences in feeding rates, length of feeding sequences, or quantity and quality of food given at the nest by the adults. We were able to measure the first two variables using blinds. Ninety-nine feeding bouts of chicks aged 1–10 days were observed in both states. There was no significant difference between the number of times chicks were fed per hour in New York and New Jersey ($t = 0.56$, N.S.) or between the length of feeding bouts ($t = 1.7$, N.S.).

The exact cause of individual chick loss was difficult to ascertain. Chicks that disappeared before 10 days of age were presumed to have been preyed upon, since they normally do not leave the nest before that age. No dead chicks up to 10 days were found during daily searches of the vegetation; perhaps they were scavenged by rats or gulls. It is not likely that adults removed dead chicks from their nests since in three nests observed from blinds, remaining chicks were brooded with a corpse in the nest. Chicks found partly eaten or bloody were also assumed to be preyed upon. As with egg loss, predation on chicks was higher in New York (31%, $N = 27$) than in New Jersey (10%, $N = 13$).

In New Jersey, six (5%) chick deaths were the direct result of a heavy rainfall (2.6 cm) accompanied by low temperatures (5.6°C below the daily mean) on 12 June. There was less total rain during the period of chick development in New York (6.4 cm) than in New Jersey (9.4 cm), but rain fell on 17 of those days in New York compared to 8 days in New Jersey. Perhaps some chick deaths were caused by exposure in New York. Williams (1975) reported a 27% loss of Glossy Ibis chicks during one hurricane in Virginia.

Twenty-eight chick deaths (32%) in New York and 18 (14%) in New Jersey were not accounted for by predation or adverse weather. These chicks were found dead in or near their nests. Most of these chicks, especially the third chick in a nest, probably died of starvation. No third chicks in broods of 3 survived in New York and only 37% of third chicks survived in New Jersey. The third chicks in New York were consistently below the mean weight at any age. By the time the third egg hatched in New York, the first chicks weighed 70–261 g ($N = 7$ nests). Smaller chicks were unable to compete with the older, larger chicks for food. In 20 feeding bouts of chicks up to 15 days old in New York and New Jersey, the oldest chick was fed 66 times, the middle chick was fed 39 times, and the youngest fed only 18 times ($\chi^2 = 30.7$, $P < .001$).

In New York, there was no significant difference between the number of chicks raised per nest when the initial brood was 1, 2, or 3 ($F = 0.92$, N.S.). A pooled value gives 0.85 chicks raised per nest. In New Jersey, significantly more young were raised in broods of 2 and 3 than in single broods ($F = 6.66$, $P < .005$), but the same number of young was riased per nest when the initial brood was two or three chicks (1.48, Table 1).

Overall nest success.—Of the nests originally incubated in New York, only 0.43 chicks fledged per nest. This is significantly fewer than in New Jersey, where 1.09 chicks fledged per nest (Table 1A). Because of predation and unsuccessful eggs, only 40% of the original nests in New York had at least one egg hatch. Due to predation, starvation, and inclement weather, only 20% of the original nests in New York and 59% in New Jersey had at least one chick fledge.

Discussion

The differences in the nesting success of the Glossy Ibis between the New York colonies in 1974 and the New Jersey colonies in 1975 could reflect intra-area or yearly variation. Fewer (minus 37%) ibises bred on Long Island in 1974 than in 1973 (Buckley and Davis 1973). Numbers of breeding ibises increased in 1975 to the 1973 levels (Buckley et al. 1975). A low food supply in New York during 1974 is indicated by the chick weights, which were less even though feeding frequency and duration were not different from New Jersey. Perhaps this postulated low food supply prevented many ibises from breeding in 1974. Some species lay smaller clutches when food is below normal (see Klomp 1970), which might account for the significantly smaller clutch size in New York.

Hatching was asynchronous in both areas, which is an adaptation to an unpredictable food supply for the young at the time of laying, and will operate through starvation to reduce the brood size to the number the adults can feed (Lack 1947). In poor food years, the last hatched chick(s) will quickly starve, but in good years, all will be raised (Lack 1954). In New York, many chicks probably died of starvation and all third chicks died. In New Jersey, where higher chick weights might indicate a greater food supply, fewer chicks probably died of starvation and 63% of the third chicks died. Starvation has also been reported to be an important factor in chick mortality in other Ciconiiformes, such as the Spoonbill (*Platalea leucorodia*) (Vespremeanu 1968), Louisiana Heron and Snowy Egret (Jenni 1969), Great Blue Heron (*Ardea herodias*) (Pratt 1970), Cattle Egret (Blaker 1969) and the Grey Heron (*Ardea cinerea*) (Owen 1960).

The degree of asynchrony in hatching should indicate the extent of variability in the food supply (Hussell 1972). This would account for the significantly longer interval between the hatching of the first and third eggs in New York. Low temperatures and heavy rains during egg-laying might also have been a factor, since low temperatures are known to delay the laying of the second or third egg in swifts (*Apus apus*) (Weitnauer 1947). Even though adults in New York were unable to deliver adequate amounts of food, the feeding rate and length of feeding bouts were not different from those in New Jersey. These behaviors appear stereotyped and are not modifiable with clutch size and asynchronous hatching to the prevailing conditions.

In both New York and New Jersey most egg and chick loss was due to predators (gulls and crows; possibly rats and night herons). These rates are comparable to predation in other mixed heronries reported by Teal (1965), Baker (1940), and Taylor and Michael (1971). Crows have been reported to be serious predators in heronries (e.g. Baker 1940, Stoner 1942, Dusi and Dusi 1968). There have been no reports of Herring Gulls as predators of Ciconiiform chicks, although they are known to prey upon other species (Harris 1965, Parsons 1971) and upon their own nestlings (Hatch

1970). In the White-faced Ibis (*Plegadis chihi*) in Utah, 22% of all eggs and 15% of all chicks were preyed upon by Franklin's Gulls (*Larus pipixcan*) (Kotter 1970).

It is not known if the nesting success in New York and New Jersey is typical for the edge of the breeding limit for ibises, or at what age ibises first breed; both factors would contribute to understanding the rapid range expansion. Some Glossy Ibises may breed after their first year, for an ibis color banded as a chick in New York was observed building a nest the next year in Maine, the current northern breeding limit. The breeding expansion of the Glossy Ibis has been characterized by the initial appearance of only a few pairs (see Hailman 1959, Post 1962); perhaps ibises from range edges help establish colonies further north. In order for a species to expand, extrinsic factors (e.g. climate, predators, habitat), which usually work against expansion, must exert less of an effect than intrinsic factors (e.g. rate of increase, population density, age structure) (Stepney and Power 1973). Ibises' rate of increase and the early age at which they may breed contribute to making them an expanding species, but the rate of increase in any one colony depends on the factors considered in this paper: food availability, predation and environmental conditions.

ACKNOWLEDGMENTS

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George Lowery, a Past-President of the A.O.U., passed away on 19 January 1978. A **Lowery Memorial Fund** has been established to provide an endowment from which expenses of research and publication by the staff, students, and associates of the LSU Museum of Natural Science may derive support. Persons wishing to contribute to this fund may do so through the **LSU Foundation, 122 Systems Building, Louisiana State University, Baton Rouge, Louisiana 70803**. Indicate that contributions are intended for the Lowery Memorial Fund.

SOME CHARACTERISTICS OF CONDITIONED AVERSION IN RED-WINGED BLACKBIRDS

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ABSTRACT.—Red-winged Blackbirds (*Agelaius phoeniceus*) were observed while feeding on food treated with methiocarb for each minute of 5-min exposure periods on 5 successive days. Feeding decreased during the first exposure, but examination of the data for exposures 2–5 indicated that at least two exposures are necessary for formation of a conditioned aversion. Tests on the individuals of six groups of birds each tested at a different interval (1 day; 1, 2, 4, 8, 16 weeks) after learning an aversion to a treated food indicated little extinction of the aversion. The experiment indicated that much of the extinction is due to the effects of testing conditions and not methiocarb. Another experiment demonstrated that red-wings can recognize the absence of methiocarb from their familiar food as well as recognize it in different food. *Received 8 November 1976, accepted 2 July 1977.*

CONDITIONED taste aversions have received extensive study by psychologists (Rozin and Kalat 1971), principally because learning can take place after a considerable interval (several h) between sampling the food and becoming ill and because the aversion develops after only one or several pairings of the food and illness. The more recent extensions of some of the principles of taste-aversion learning to birds (Capretta and Moore 1970, Wilcoxon et al. 1971, Shettleworth 1972, Brett et al. 1976) have led to experiments suggesting that this phenomenon may be useful in developing repellents for use against depredating birds (Rogers 1974). Recent research (Schafer and Brunton 1971, Guarino 1972) has shown that methiocarb [3,5-dimethyl-4-(methylthio) phenol methyl carbamate (Mesurol®)] (Chemagro Division, Baychem Corp.) is a promising bird repellent that acts by creating a conditioned aversion in those birds that consume it (Rogers 1974).

The present experiments were designed to examine several characteristics of conditioned aversions in an economically-important avian species, the Red-winged Blackbird (*Agelaius phoeniceus*) (Dyer 1967, Dolbeer 1975). The specific questions asked were: (1) what is the time course of development of a conditioned aversion, both within the first exposure and across several exposures; (2) what is the duration of an aversion once it has been learned; and (3) does this species form an aversion that is specific to the aversive agent-food combination or to one or the other of these elements?

GENERAL METHODS

Male Red-winged Blackbirds of various ages were trapped at the Patuxent Wildlife Research Center, Laurel, Maryland, and kept in captivity for at least 2 weeks prior to use in experiments. They were individually housed in cages 36 × 61 × 41 cm high, in a room with a temperature of approximately 23°C and a light cycle of 6 h light, 18 h dark. The shortened light period was employed to maximize the birds' feeding rate without reducing the total quantity of food consumed. Earlier preliminary experiments demonstrated that a 6-h period was the shortest time during which the birds could readily obtain enough food to maintain initial body weights (Rogers 1974). All testing was carried out during a 5-min (Experiment 1) or a 1-min (Experiments 2 and 3) period during the first hour of light. This testing period

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[1] The author is assigned to the Pennsylvania Field Station of the Denver Wildlife Research Center, U.S. Fish and Wildlife Service, Laurel, Maryland.

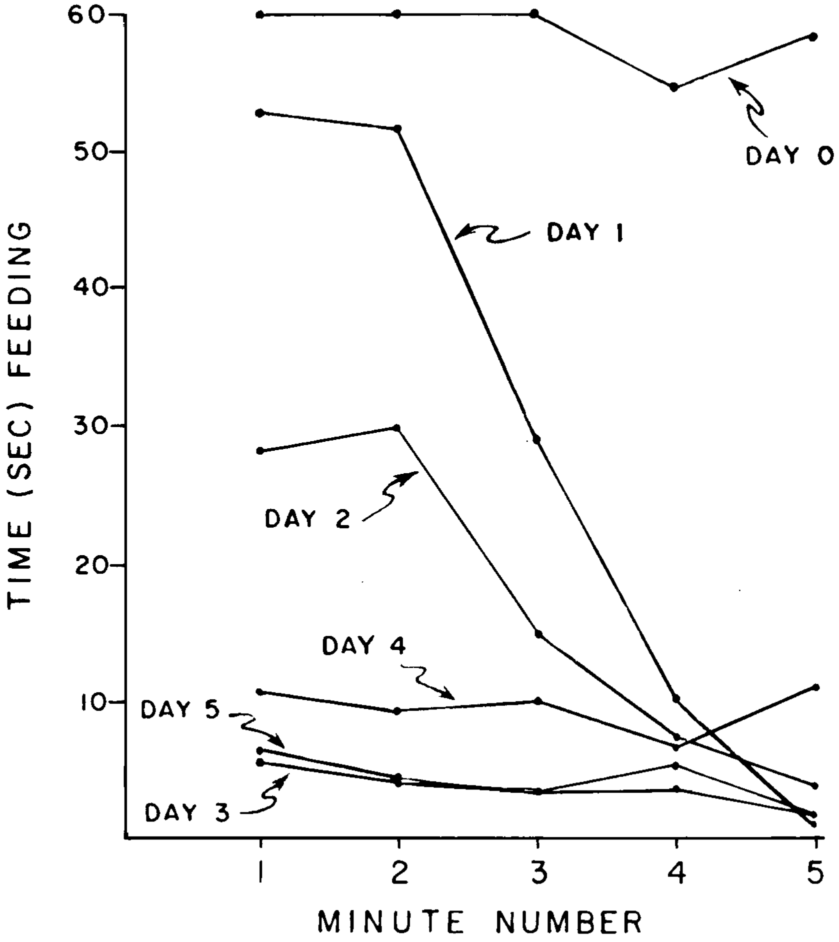

Fig. 1. Feeding responses of eight male Red-winged Blackbirds in each minute of 5-min testing periods on successive days. Day 0—feeding on untreated food. All other Days—feeding on food treated with 0.07% methiocarb.

represented the first exposure to food on the test days. Food was always available *ad libitum* for the last 5 h of the light period from a food cup located at the front of the cage. Water was always available from a graduated drinking tube at the back of the cage. To reduce spillage, each food cup (diameter 7.5 cm) was placed within a larger cup (diameter 11.3 cm). This larger cup caught the spillage from the smaller one during normal feeding activity.

The birds were maintained on a diet of Purina Game Bird Flight Conditioner (GBFC) from Ralston Purina Company. [Use of commercial products does not imply endorsement by the U.S. Government.] The test diet was prepared by thoroughly mixing in the food (usually GBFC) 0.07%, by weight, methiocarb. All birds used were experimentally naive at the beginning of each experiment.

Data were obtained by observing the individual birds via remote television monitor, and recording for each minute of the test period (1 or 5 min) the amount of time spent feeding, the number of visits to the foodcup (whether or not feeding occurred), and the number of drinking bouts. The food was weighed both before and after the test period.

EXPERIMENT 1

This experiment was designed to examine the time course of the response to methiocarb upon first exposure, as well as to examine the effect of the repellent on the

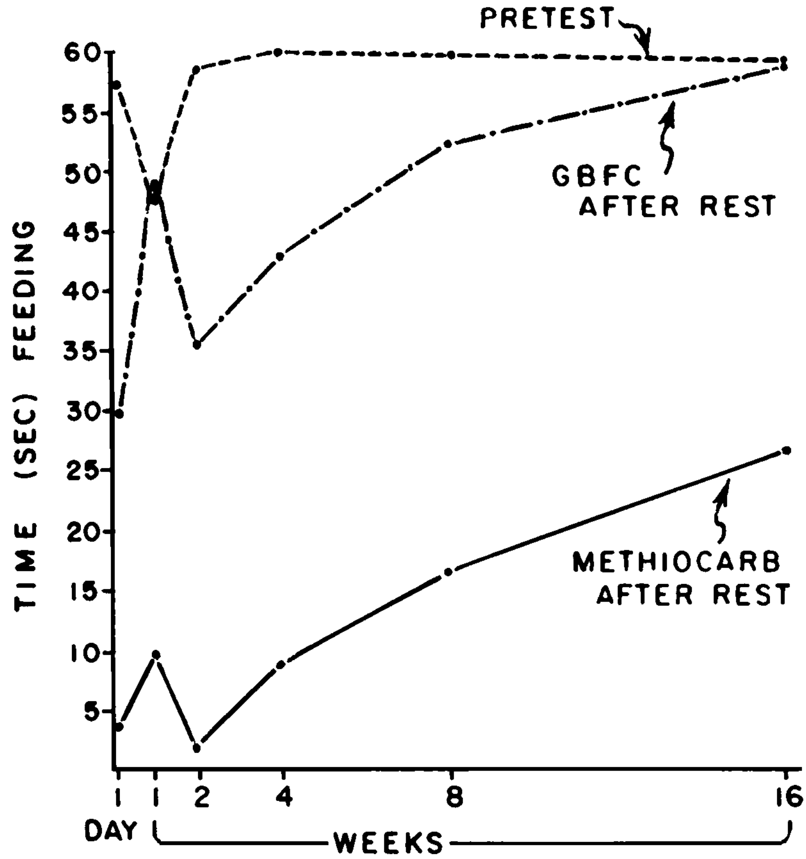

Fig. 2. Feeding responses of 6 groups of 9 male Red-winged Blackbirds at various intervals after formation of a conditioned aversion to 0.07% methiocarb. Top curve represents feeding on untreated food before training. Middle curve represents feeding on untreated food after the rest interval, the day preceding retesting with methiocarb. Bottom curve represents feeding on treated food after the rest interval.

feeding behavior of the birds during successive daily 5-min exposures to the treated food. After habituation to the test situation for several days eight birds were individually observed for each minute of a 5-min feeding period with untreated GBFC (Day 0). On Days 1 through 5, they were observed for each minute of a 5-min exposure to 0.07% methiocarb in GBFC.

The feeding responses of this group of red-wings on succeeding daily exposures to methiocarb-treated food are shown in Fig. 1. A two-way (day × min) analysis of variance with repeated measures indicated that successive exposures to the repellent significantly altered the daily pattern of feeding during the test period (F = 102.38, 5/35 df, $P < 0.001$) as well as an effect of minutes within days (F = 19.69, 4/28 df, $P < 0.001$). The interaction was also significant (F = 9.61, 20/140 df, $P < 0.001$) indicating a different pattern of response on successive days. The curve for Day 1 indicates that, on initial contact and for approximately 2 min, the feeding rate is near normal (Day 0 curve); by the third minute, however, a great decrease in feeding rate occurs and the birds are feeding at a rate less than one-half of normal. They have essentially stopped feeding by the fifth minute of the first exposure. This decrease in feeding on the treated food during the first exposure may be due to one or a combination of factors. It may be due solely to the intoxicating effect of methiocarb—they are simply too sick to eat. It also may be due to the birds becoming ill and associating the illness with some sensory aspects of the treated food (forming a conditioned aversion). Examination of the curves for Days 2 through 5 shed some light on these not-completely-independent hypotheses. If learning was not taking place on or as a result of the first-day experience, the patterns of the succeeding exposures would all be the same. They are not. The feeding rate for Day 2 (min 1) begins at a point about one-half of that on Day 1. Thus, the descending curves for Days 1 and 2, when compared with the rather flat curves for Days 3, 4, and 5, indicate that, under these conditions, at least two successive daily 5-min exposures are necessary before Red-winged Blackbirds learn a conditioned aversion to methiocarb. An alternative explanation might be that the birds became sicker and sicker each day as a result of the cumulative effects of the methiocarb. This probably is not the case because the birds behaved in an otherwise normal fashion and ate the untreated food immediately when it was offered.

EXPERIMENT 2

The first experiment indicated that red-wings cease feeding on methiocarb-treated food very soon after encountering it, and that relatively few exposures are necessary to create a conditioned aversion to a food so treated. For practical development and use of conditioned aversion as a repellent response, it is important to know the duration of the conditioned aversion once a bird learns it.

The individuals of 6 groups of 9 birds each were pretested for a 1-min period with untreated GBFC and then trained to avoid the methiocarb-GBFC by allowing them 1-h exposures to it on 4 consecutive days. On the fifth day, all were tested by observing them for the first 1-min period of the day while feeding on treated food to verify that they had formed an aversion to methiocarb. Each group was then allowed a prescribed length of time (1 day; 1, 2, 4, 8, or 16 weeks) before the individuals were retested to examine the time span of retention of the aversion. During this time, they were left undisturbed and had *ad libitum* access to the untreated GBFC and water during the light (6 h) portion of the day. At least 4 days before retesting, each group was returned to the testing room and observed for a 1-min period of feeding on untreated GBFC as an estimate of possible alteration in feeding behavior during the interim or as a measure of retention of learning about the testing conditions. On the next day, all were tested by observing them for a 1-min period while they had access to the methiocarb-treated food.

The bottom curve in Fig. 2 indicates the ability of the blackbirds to retain a conditioned aversion. There was a significant difference between the individuals as a function of time since training ($F = 5.5$, 5/47 df, $P < 0.001$). Up to 4 weeks post-training, there was no significant loss of the conditioned aversion (Duncan's New Multiple Range Test, $P = 0.01$). After 4 weeks between training and retesting the aversion was somewhat diminished. A comparison of the feeding rate on untreated food prior to any exposure to methiocarb (top curve, Fig. 2) with that on treated food after training and the waiting period (bottom curve, Fig. 2), indicates that even after 16 weeks the earlier aversive experience caused the birds to feed at less than one-half of their normal rate on the untreated food.

An interesting phenomenon is apparent from the middle curve in Fig. 2. This curve represents time spent feeding on untreated GBFC for the 5-min test period on

TABLE 1. Feeding response in a 1-min exposure of eight male Red-winged Blackbirds to untreated foods and foods treated with 0.07% methiocarb. The treatments are arranged in order of presentation from top to bottom[a]

Treatment	Time spent feeding (s ± SEM)
Pretest untreated GBFC	$57.9 \pm 2.1^{*+}$
First exposure methiocarb in GBFC	$59.5 \pm 0.5^{*}$
Methiocarb in GBFC after training	5.1 ± 3.4
Untreated GBFC	$45.5 \pm 7.0^{+}$
Untreated rice	$48.5 \pm 7.0^{*+}$
First exposure methiocarb in rice	17.4 ± 3.9

[a] All means not marked with the same symbol are significantly different from each other (Duncan's New Multiple Range test) ($P = 0.05$)

the day immediately before retesting with the methiocarb-treated food. Since this measure was taken after training with the repellent and after the prescribed rest period it probably represents the effect of learning about the testing conditions alone. It suggests that most of the increased feeding on the treated food after the longer time periods (8 and 16 weeks) may be due to extinction of learning about the testing conditions rather than extinction of the conditioned aversion.

EXPERIMENT 3

The results of the first two experiments demonstrated that red-wings are capable of learning an aversion to methiocarb when it is presented in their familiar food, and that they can recognize methiocarb in their familiar food when it is presented at a subsequent time. The experiments did not answer the question of what cue(s) the subsequent aversion was based on.

Eight birds were trained to avoid methiocarb as in Experiment 2, and the aversion was verified in a 1-min test on Day 1. On Day 2, they were retested with untreated GBFC to test whether they would recognize the absence of methiocarb. During Days 3 through 6, the group was allowed *ad libitum* access to finely-ground, unhulled dry rice. On Day 7, their consumption of this material was verified in a 1-min test. Finally, on Day 8, the birds were individually tested for 1 min with methiocarb-treated rice.

The results of this series of tests are shown in Table 1. An analysis of variance with repeated measures indicated an overall difference in feeding behavior when the birds were confronted with the various foods ($F = 28.7$, 5/35 df, $P < 0.001$). Duncan's New Multiple Range Test ($P = 0.05$) was used to identify the individual differences between treatment means (Table 1).

The foregoing data indicate several characteristics of the response of red-wings to methiocarb. Their reaction in the first minute of their very first exposure to methiocarb in their familiar food, as demonstrated in Experiment 1, and repeated in this experiment, is to feed normally. The birds do not respond immediately to the sensory characteristics of methiocarb alone. They then learn to associate one or more of the sensory aspects of the methiocarb, and not the food, with the aversive experience. This has been demonstrated because they recognize the absence of methiocarb and feed at a rate not statistically different from that prior to training. The data from this experiment indicate that red-wings are capable of responding to the presence of methiocarb on the basis of its chemosensory characteristics, probably taste, alone. It is possible that the birds can differentiate between treated and untreated GBFC on the basis of color because the color of GBFC mash lightens when methiocarb is added to it. Ground rice, however, is white and pure methiocarb is white; thus, there is no visual difference between treated and untreated rice. The subjects *did* discriminate between the treated and untreated rice. Since red-wings, as well as most other passerines, do not regulate their behavior on the basis of odors (Kare and Rogers 1976) they were probably not responding to the odor of methiocarb in the treated diets. The behavior of the birds when confronted with methiocarb-treated rice also suggests that they were responding to its taste. All birds initially showed almost no latency to approach the food cup and begin feeding, but after a few pecks or probes at the food, they ceased feeding activity altogether.

DISCUSSION

Under the conditions of these experiments, approximately two successive daily 5-min exposures to methiocarb-treated food are necessary before Red-winged Blackbirds learn an aversion. Once the aversion is formed, it persists relatively unchanged for periods up to 4 weeks after training and is not completely extinguished at 16 weeks. Further work will be necessary to differentiate fully between the importance of situational cues (testing conditions) and those cues provided by the aversive agent-food combination. Additionally, red-wings apparently can react to the taste of an aversive agent when it is presented in a food other than that in which it was initially presented.

Some interesting comparisons can be made between the results of these experiments and experiments that examine conditioned taste aversions in other species. Under the conditions of my experiments, red-wings apparently require longer to learn an aversion than the traditional one-trial learning exhibited by laboratory rats and Bobwhite Quail (*Colinus virginianus*) (Wilcoxon et al. 1971). This may be the result of a combination of two factors that have not yet been resolved. First, with few exceptions, all experiments in taste-aversion learning are concerned with poisoning an animal after the ingestion of a *novel* stimulus. In my experiments, methiocarb was presented as an additive in the *familiar* food. Second, Wilcoxon et al. (1971) have demonstrated that birds more readily learn aversions to visual cues than they do to taste cues alone. Although visual cues were not controlled in my experiments, the addition of methiocarb to the familiar GBFC makes only a minor (to me) change in the color of the food. The difference in the results reported here most likely arises from a combination of the familiarity of the food and the relative non-salience of the cues involved.

Another major difference in my results from those usually reported for rats is that rats commonly refuse to eat food that has been associated with toxic consequences in the past. This frequently occurs even after the poison has been removed from the food (Galef and Clark 1971). The results of Experiment 3 indicate that red-wings can not only recognize when the illness-producing agent has been removed from the food but also do not refuse to consume this food once the agent has been removed. This may be a result of the difference between the reactions of rats and red-wings once they have been poisoned from a diet. Rats frequently fail to approach the poisoned diet (Galef and Clark 1971) whereas the birds in my experiments usually approached the food and were commonly observed probing and manipulating the treated food while not actually eating it. Consequently, they probably have the opportunity to recognize the absence of the toxic material. The difference may also be due to the nature of the test. In my experiments, testing was performed with the intoxicant presented in a familiar food (GBFC). The test period was always followed by 5 h of *ad libidum* access to untreated GBFC. Though the two (treated and untreated GBFC) were not present simultaneously, untreated GBFC was offered to the birds soon after each test with the treated GBFC. Thus, the birds had many opportunities to learn the difference between treated and untreated food. In most other experiments, the animals only experience the novel stimulus when it is paired with the aversive consequences.

Wild birds might not be expected to show such an impressive ability to retain an aversive response. The birds in this experiment were trained and then taken to another room to wait for retesting. Under these conditions, there was probably a minimum of interfering stimuli. When the birds were brought back to the testing room, they probably were associating many of the cues produced by the testing situation in addition to the sensory aspects of the food with the previous aversive experience. Wild birds would probably not have as many different cues available to associate with the aversive situation. These experiments demonstrate that, given the right cues, red-wings can retain the memory of an aversive experience for a considerable time.

The results of my experiments suggest several implications on the use of the conditioned aversion as a response to be exploited in the development and use of repellents for depredating bird species. First, it is reasonable to predict at least a low level of damage to treated crops, since I have shown that several exposures to the treated food are necessary for the development of an aversion to methiocarb when it is used on a food familiar to the birds (a condition that would obtain in most crop-depredation situations). Second, the indication that red-wings can recognize the absence of the repellent material and do not refuse to eat a previously treated food would seem to indicate that the repellent would need to be present in effective concentration during the susceptible period of a crop. This also might lead to increased damage to other crops or those of the same type that were, for one reason or another, untreated.

ACKNOWLEDGMENTS

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The **North American Conference on Common Loon Research and Management**, sponsored by the National Audubon Society and hosted by Syracuse University, was held 12–14 August 1977 at the Minnowbrook Conference Center, Blue Mountain Lake, N.Y. Priorities determined by the participants included: (1) establishment of an informal working group to serve as a clearing-house for information on research and management efforts; (2) collection of historical loon nesting records for assessment of recent range contraction or expansion by this species; (3) coordination and standardization of breeding surveys and an effort to document the current breeding status of the loon, particularly in the northeastern U.S.; and (4) expanded research, including increased banding efforts and initiation of a winter banding program.

The working group, consisting of Judith W. McIntyre of Syracuse University, Richard L. Plunkett of the National Audubon Society, and Rawson L. Wood of the Loon Preservation Committee of the Audubon Society of New Hampshire, plans another meeting next year. Requests for conference summaries and other inquiries may be directed to the coordinator, **Judith W. McIntyre, Biology Department, Syracuse University, Syracuse, N.Y. 13210.**

The Linnaean Society of New York, as part of its centennial celebration, will host the Second Annual Meeting of the **Colonial Waterbird Group** at the American Museum of Natural History in New York City on **20–23 October 1978**. The Linnaean Society will sponsor a symposium of invited papers on factors affecting productivity in colonial species on 21 October and the morning of 22 October. Submitted papers will be given on the afternoon of 22 October and on 23 October. For information on contributing a paper, write to Dr. P. A. Buckley, **North Atlantic Regional Office, National Park Service, 15 State Street, Boston, Mass.** For registration information write to Miss Helen Hays, Department of Ornithology, American Museum of Natural History, Central Park West at 79 Street, New York, N.Y. 10024.

WEATHER-DEPENDENT FORAGING RATES OF WINTERING WOODLAND BIRDS

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ABSTRACT.—Foraging rates of birds wintering in an Ohio woodlot were dependent on proximate weather conditions. Increased wind velocity and decreased temperature resulted in increased time stationary (s/min), increased number of stops/min, and decreased distance travelled (m/min) for the Downy Woodpecker, Carolina Chickadee, Tufted Titmouse, and White-breasted Nuthatch. Wind velocity effects were heightened as temperature decreased. Analyses of avian community structure based on foraging behavior below the critical thermal environment are now suspect. Future studies of competition in winter must consider the impact of weather. *Received 1 October 1976, accepted 1 January 1977.*

THIS paper concerning weather-dependent foraging rates is part of a series (Grubb 1975, in press) on the effects of cold stress on avian feeding niches. Cody (1968, 1974) has used foraging rates as one means of analyzing community structure. Importantly, Cody's records were taken at the height of the breeding season when extremes in weather conditions were never present (M. L. Cody, pers. comm.). This paper explores the modification of species-typical foraging rates by winter weather.

Physiological models (e.g. Moen 1968, Porter and Gates 1969) suggest that below the lower critical temperature (about 25°C for small birds, Helms 1968), metabolic energy consumption should be directly related to the rate at which birds move while foraging. With more rapid progression a bird is, in effect, foraging in higher wind velocities, increasing convective heat loss (Porter and Gates 1969), and consequently energy output. Assuming that selection has favored behavioral patterns that allow birds to husband energy reserves while foraging "below" the critical thermal level (*sensu* Moen 1968), I tested the prediction that increasing wind velocities and decreasing temperatures in winter cause foraging birds to slow their average rate of movement and to spend more time stationary. Support for this reasoning comes from the rates of movement of wintering hereford cattle (*Bos taurus*), which have been shown to be negatively correlated with wind velocity (Malechek and Smith 1976): Because laboratory findings indicate that the metabolic cost of low temperature is moderated by artificial insolation (Lustick 1969, Lustick et al. 1970), I also checked for higher rates of foraging in sunlight than under cloud cover.

METHODS

From November to March 1975–76, I watched birds foraging in a 26-ha beech-maple woodlot in Bennington Township, Morrow County, Ohio. I watched only the four most abundant species, the Downy Woodpecker (*Picoides pubescens*), Carolina Chickadee (*Parus carolinensis*), Tufted Titmouse (*P. bicolor*), and White-breasted Nuthatch (*Sitta carolinensis*), and kept separate records for the woodpecker sexes. During each 1–2 h study session, I walked different portions of the study area in randomized order. Foraging behavior was characterized with a slightly modified Cody (1968) technique. Individual birds were followed for 100 s intervals timed on one stopwatch. With a second stopwatch, I accumulated the number of seconds the bird was stationary during the interval. Concurrently, I tallied the number of times the bird stopped during the foraging sequence. Observation was terminated whenever a bird commenced activity (e.g. preening, social interaction) other than foraging before conclusion of 100 s. At the close of each bout, I estimated the length of the 100-s foraging route. The resulting foraging records do not differentiate among types of movement (walking, flying). From these sightings I calculated time spent stationary (s/min), number of stops/min, and distance travelled (m/min).

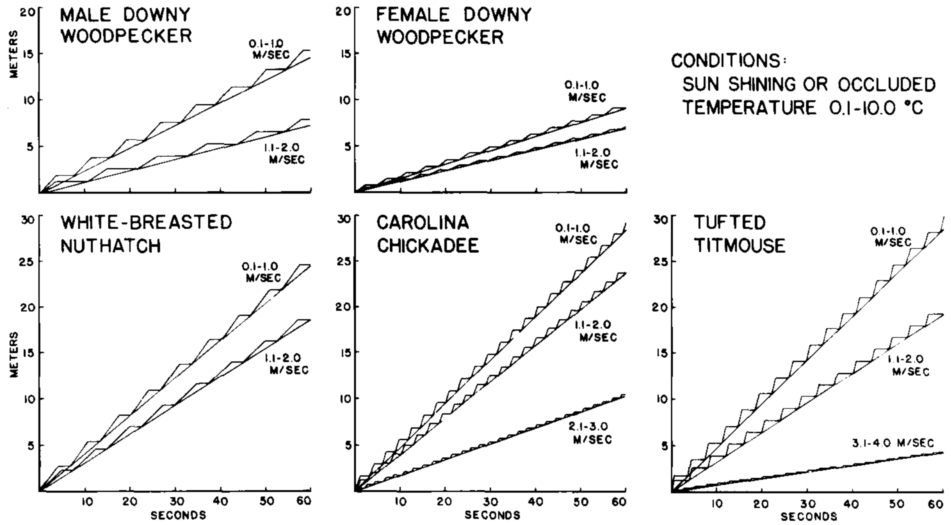

Fig. 1. Wind velocity-dependent foraging curves for four bird species wintering in a deciduous woodlot. Wind velocities are shown in the figure. Each "sawtooth" consists of a sloped component representing the rate of an average individual movement and a flat component denoting the time span of an average stop. The diagonal common to all sawteeth marks the average foraging speed over 1 min.

Immediately following each sighting, I noted whether the sun was shining (defined as the presence of shadows) and measured wind velocity with a portable anemometer 2 m above the ground away from shrubs. Temperature was measured every hour and relative humidity at the end of each observation session; all readings were taken in the shade 2 m above the ground. Except for avoiding precipitation, I pursued field work regardless of weather. Thus, sample size differences throughout this report reflect prevailing weather conditions.

Relative humidity remained within such narrow limits during the study (range, 69–78%) that I lumped sightings irrespective of humidity when considering other weather variables. I determined the effect of sunlight, wind velocity, or temperature on foraging behavior by grouping sightings so as to hold the other variables constant or within narrow ranges. Analyses were restricted to sample sizes of at least 10.

RESULTS

I tested the effect of solar radiation on foraging in the five bird types across a total of 15 combinations of 10°C temperature ranges and 1 m/s wind velocity ranges. In no case did a significant difference occur between sunny and cloudy conditions in time stationary (s/min), stops/min, or distance (m/min) (t-tests, $P > .05$), nor were any clear trends apparent. I therefore grouped sightings irrespective of sunlight when examining wind and temperature.

Increased wind velocities slowed foraging rates (Fig. 1, Appendix 1). For instance, in temperatures from 0.1–10.0°C, the Tufted Titmouse spent 45.8 s stationary, stopped 16.5 times, and advanced 28.7 m during each minute of foraging in 0.1–1.0 m/s (0.2–2.2 mph) wind velocities, but remained motionless for 52.7 s, made 22.9 stops, and covered only 4.4 m per min in the higher wind speeds of 3.1–4.0 m/s (6.8–8.8 mph). Such changes in feeding technique were followed by the other species, occasionally significantly, and are illustrated with a sawtooth feeding graph (Fig. 1) styled after those of Cody (1968). The long diagonals denote overall progression during feeding. Each sawtooth consists of a more steeply sloped line representing an average individual movement and a component of zero slope marking the length of an aver-

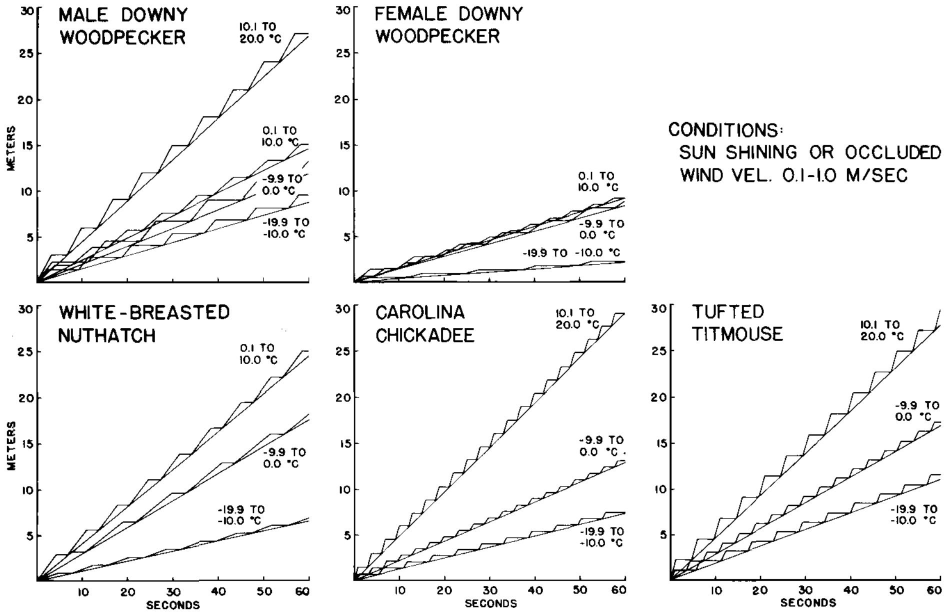

Fig. 2. Temperature-dependent foraging curves for four bird species wintering in a deciduous woodlot. Temperatures are shown in the figure. The "sawtooth" as in Fig. 1.

age stop. In general, higher wind speeds caused birds to decrease their overall progression through the woodland and either increase the number of short, rapid movements (female woodpecker, chickadee, titmouse) or retain about the same number of moves, but make them more slowly (male woodpecker, nuthatch).

Changing temperatures profoundly modified foraging (Fig. 2, Appendix 2). In wind velocities of 0.1–1.0 m/s, decreasing temperatures caused significantly increased time stationary, decreased number of stops, and reduced overall travel through the woodlot. These effects were often dramatic, e.g. a 30°C increase in temperature quadrupled the foraging speed of chickadees. Figure 2 summarizes graphically the increase in foraging speed with elevated temperature.

Linear regressions of chickadee and titmouse foraging rates on temperature for two wind velocity intervals are plotted in Fig. 3. The increasingly important effect of wind velocity as the temperature falls is apparent, especially for the titmouse. Notice how the weather conditions involved appear to influence the smaller chickadee more drastically, although the slopes are not statistically significantly different ($P > .05$). Extending the regression to the abscissa suggests that the chickadee's foraging rate should theoretically be driven to zero before that of the titmouse, at least in 0.1–1.0 m/s wind speeds.

Discussion

My criterion for sunshine (visible shadows) probably did not provide a fair test of solar radiation effects. Unfortunately, my manner of record keeping does not permit me to discard the intermediate cases of weak cloud cover and to compare sunlight in a cloudless sky with heavy overcast. I have previously found an effect of solar radiation on other foraging parameters (Grubb in press) and believe the same could still be true for feeding rates.

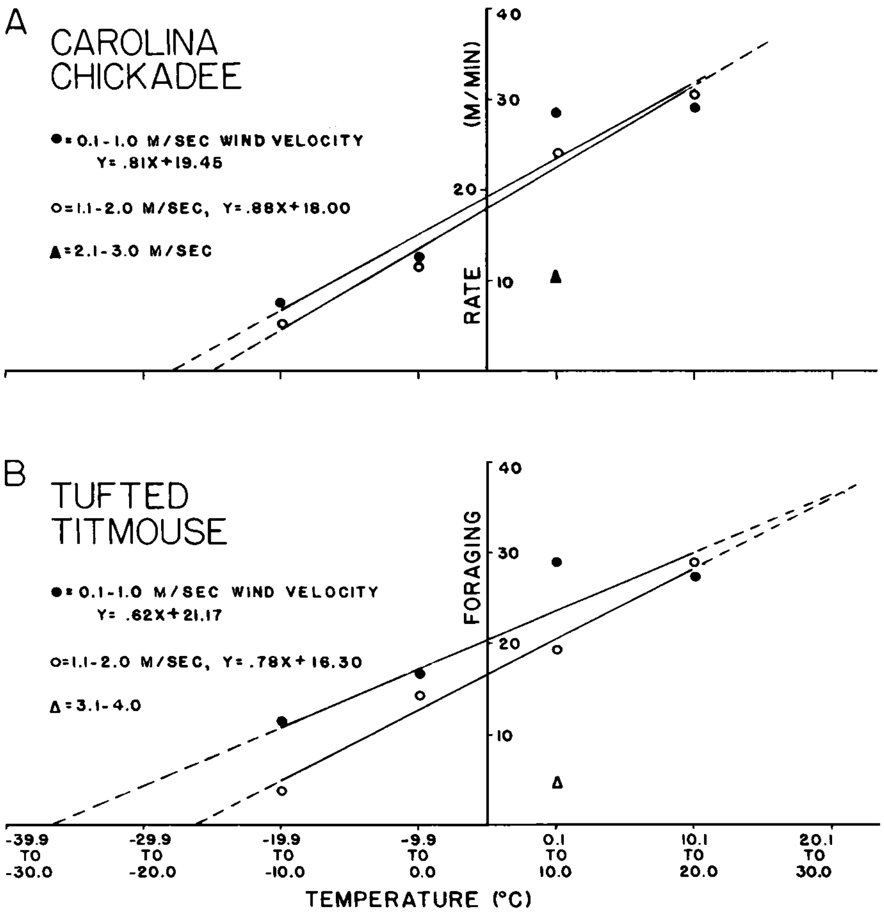

Fig. 3. Regression lines of foraging rate on temperature at two wind velocity ranges for two bird species wintering in a deciduous woodland.

Wind- and temperature-dependent foraging rates appeared influenced by shifts in foraging substrate. For instance, in higher wind velocities, the branch- and twig-foraging chickadee and titmouse descended more often to the ground to probe the leaf litter for fallen beech mast. This tactic led to the minutely-sectioned sawtooth curves characterized by many small, short hops (Fig. 1). By contrast, with worsening conditions male Downy Woodpeckers descended from moderately rapid foraging on small branches in the canopy to the leeward sides of large-diameter trunks and fallen logs (Grubb in press) where they engaged in rather sedentary sessions of cavity excavating (Figs. 1 and 2). The increased surface area of substrates used in harsher weather, rather than the weather itself, might sometimes account for a decrease in foraging rate. A bird looking for food should be able to scan more surface area without having to move while foraging on the ground, say, than on a twig. Further study is needed to determine if weather *per se* or a weather-induced increase in substrate surface area is the proximate cause of reduced foraging rates.

Analyses of avian community structure based on foraging behavior below the critical thermal environment are now suspect. In this and previous papers (Grubb 1975, in press) I have shown that such commonly employed foraging parameters as height, substrate type, tree species, horizontal distribution, and foraging rate are all labile and weather-dependent. As many bird species may be limited by winter mortality (Fretwell 1972), the necessary future studies of competition in winter must consider the vicissitudes of weather.

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APPENDIX 1. Effect of wind velocity on foraging in temperatures from 0.1–10.0°C

		Wind velocity (m/s)				
Foraging measure	Bird type	0.1–1.0	1.1–2.0	2.1–3.0	3.1–4.0	P[a]
Time stationary (s/min)	♂DW[b]	30.7 ± 14.5 (23)[c]	40.7 ± 19.2 (11)			ns
	♀DW	32.7 ± 10.7 (14)	28.8 ± 12.4 (15)			ns
	WBN	23.2 ± 10.0 (27)	21.0 ± 10.3 (15)			ns
	CC	43.2 ± 5.1 (29)	45.7 ± 4.2 (36)	45.3 ± 9.5 (10)		ns
	TT	45.8 ± 3.6 (31)	47.5 ± 7.6 (15)		52.7 ± 1.9 (10)	<.001
Stops/min	♂DW	7.6 ± 4.0 (23)	5.5 ± 4.8 (11)			ns
	♀DW	12.9 ± 11.8 (14)	14.0 ± 7.6 (15)			ns
	WBN	8.9 ± 5.4 (27)	7.9 ± 4.2 (15)			ns
	CC	21.3 ± 5.5 (29)	23.0 ± 6.0 (36)	28.2 ± 9.2 (10)		<.01
	TT	16.5 ± 4.3 (31)	14.6 ± 6.2 (15)		22.9 ± 8.8 (10)	<.01
Distance (m/min)	♂DW	14.6 ± 13.2 (23)	7.3 ± 8.6 (11)			ns
	♀DW	9.2 ± 9.4 (14)	7.0 ± 5.1 (15)			ns
	WBN	24.5 ± 26.5 (27)	19.3 ± 12.6 (15)			ns
	CC	28.4 ± 20.9 (29)	23.8 ± 14.3 (26)	10.4 ± 3.9 (10)		<.01
	TT	28.7 ± 20.3 (31)	19.3 ± 12.6 (15)		4.4 ± 3.7 (10)	<.001

[a] t-test comparisons of means from the lowest and highest wind velocity ranges available

[b] DW = Downy Woodpecker; WBN = White-breasted Nuthatch; CC = Carolina Chickadee; TT = Tufted Titmouse

[c] $\bar{X}$ ± SD(N)

APPENDIX 2. Effect of temperature on foraging in wind velocities from 0.1–1.0 m/s

Foraging measure	Bird type	Temperature (°C)				P[a]
		−19.9 to −10.0	−9.9 to 0.0	0.1 to 10.0	10.1 to 20.0	
Time stationary (s/min)	♂DW[b]	45.0 ± 15.4 (31)[c]	40.4 ± 7.2 (13)	30.7 ± 14.5 (23)	30.3 ± 13.4 (15)	<.01
	♀DW	47.0 ± 12.6 (12)	35.7 ± 16.7 (25)	32.7 ± 10.7 (14)		<.001
	WBN	25.1 ± 13.8 (17)	17.5 ± 12.3 (26)	23.2 ± 10.0 (27)		ns
	CC	51.6 ± 10.5 (19)	45.6 ± 5.5 (39)	43.2 ± 5.1 (29)	46.0 ± 4.6 (28)	<.001
	TT	52.6 ± 4.0 (16)	43.4 ± 10.1 (31)	45.8 ± 3.6 (31)	46.2 ± 4.5 (10)	<.001
Stops/min	♂DW	6.4 ± 3.2 (31)	5.3 ± 3.8 (13)	7.6 ± 4.0 (23)	8.9 ± 2.6 (15)	<.05
	♀DW	4.8 ± 2.6 (12)	6.2 ± 3.8 (25)	12.9 ± 11.8 (14)		<.05
	WBN	7.6 ± 3.3 (17)	5.5 ± 2.8 (26)	8.8 ± 5.4 (27)		ns
	CC	10.8 ± 8.1 (19)	18.7 ± 6.4 (39)	21.3 ± 5.5 (29)	19.8 ± 6.1 (28)	<.001
	TT	10.6 ± 5.8 (16)	16.6 ± 5.4 (31)	16.5 ± 4.3 (31)	12.3 ± 3.9 (10)	ns
Distance (m/min)	♂DW	8.9 ± 13.1 (31)	12.0 ± 14.1 (22)	14.6 ± 13.2 (23)	27.0 ± 20.1 (15)	<.001
	♀DW	2.2 ± 2.2 (12)	8.3 ± 8.4 (25)	9.2 ± 9.4 (14)		<.05
	WBN	6.6 ± 4.8 (17)	17.7 ± 13.9 (26)	24.5 ± 26.5 (27)		<.01
	CC	7.4 ± 8.4 (19)	12.9 ± 9.7 (39)	28.4 ± 20.9 (29)	29.1 ± 16.1 (28)	<.001
	TT	11.2 ± 8.6 (16)	17.0 ± 9.5 (31)	28.7 ± 20.3 (31)	27.8 ± 8.7 (10)	<.001

[a] t-test comparisons of means from the lowest and highest temperature ranges available

[b] DW = Downy Woodpecker; WBN = White-breasted Nuthatch; CC = Carolina Chickadee; TT = Tufted Titmouse

[c] $\bar{X} \pm SD(N)$

APOSTATIC SELECTION AND KLEPTOPARASITISM IN THE PARASITIC JAEGER

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ABSTRACT.—The economics of predator avoidance suggest that a prey can act as an apostatic selective agent on its polymorphic predator if it tends to learn an "evil image" of its most common predator more readily than of its rarer predator. Therefore the rare predator morph is expected to catch more prey and it thereby gains a relative advantage over the more common predator morph. Learning among prey that get eaten and the exclusive use of a prey population by one individual predator (territoriality) are problems which are alleviated in the case of the polymorphic klepto-Parasitic Jaegers that hunt on communal grounds. Thus in a locality in southern Iceland where the jaegers rob fish from Common Puffins, light-phased jaegers (the rare morph) were successful in 81% of their attempts whereas the dark-phased ones had a 63% success rate. These observations (based on 3–12 light-phased individuals) accord with the predictions from the apostatic selection hypothesis. To fully test the hypothesis data on the avoidance responses of hosts and the success rate of the two morphs of jaegers are needed from different populations of the Parasitic Jaeger's clinal polymorphism. *Received 15 November 1976, accepted 3 July 1977.*

IN apostatic polymorphism the morphs that stand out from the norm by virtue of their rarity have a selective advantage (Clarke 1962a, 1962b, 1969). This kind of frequency-dependent selection is believed to result from the action of predators which, when maximizing their feeding efficiency, form a "search image" of the most common morph more readily than of the rare morph (Allen 1976, Allen and Clarke 1968, Tinbergen 1960, and see Dawkins 1971). With the predator tending to overlook it just because it is rare, the rare morph gains a relative advantage over the more common morph.

It is reasonable to expect anti-predator behavior to be of selective advantage to prey (Kruuk 1964). The economics of predator avoidance suggest that a prey can maximize its protective advantage if it tends to form an "evil image" of its most common predator more readily than of its rarer predator (Arnason 1974). In this way a prey can act as an apostatic selective agent on its polymorphic predator (Paulson 1973) by responding differentially to the predator morphs. The rare morph will be less familiar to the prey and will thus have a greater hunting success (Paulson 1973).

Recognition of the predator morphs may be learned rather than fixed, which provides for flexibility to deal with changing situations. However, learning presents a problem because prey get eaten. Furthermore, if the predator is territorial, a prey individual may encounter only one of the predator morphs. There are thus two major obstacles to applying the hypothesis of apostatic polymorphism to predators.

The Parasitic Jaeger (*Stercorarius parasiticus*) appears to be an excellent species for testing the hypothesis of apostatic predator polymorphism. Although intermediates exist there are basically two morphs: light- and dark-bellied (Southern 1943). The polymorphism varies clinally with the light morph predominating in the north and the dark morph most common in the south (Southern 1943, Berry and Davis 1970) although some irregularities have been noted (Hildén 1971). O'Donald and Davis (1975 and references therein) suggest that several selective forces are involved (a minor part of which is frequency-dependent sexual selection). They conclude that the polymorphism of the jaeger is transient and that the light morph will eventually

TABLE 1. Success of dark- and light-phased jaegers in inducing puffins to drop their fish

Number of jaegers	Color of participants in a chase	Number successful	Percent successful	Total number of chases
1	Dark	441	62.6	704
1	Light	25	80.7	31
2	Dark-Dark	194	78.5	247
2	Light-Dark	29	90.6	32
3	Dark-Dark-Dark	56	76.7	73
3	Light-Dark-Dark	12[a]	80.0	15
4,5,6	Dark-Dark-Dark-Dark,-Dark,-Dark	14	73.7	19
4,5,6	Light-Dark-Dark-Dark,-Dark,-Dark	8	88.9	9

[a] This category includes a Light-Light-Dark chase, the only instance observed with more than one light-phased individual

replace the dark one. Here I propose that the polymorphism is balanced, being maintained at least partly by apostatic selection.

During a study on jaegers kleptoparasitizing Common Puffins (*Fratercula arctica*) on the south coast of Iceland (Arnason 1974, Arnason and Grant 1977, see also Grant 1971, Grant and Nettleship 1971), I noted the hunting success of the two morphs of jaegers. From late June to early September 1973 I periodically spent a whole day at the puffin cliff studying the behavior of the interactants. The puffins carried fish in the bill to feed their young in the terrestrial burrows at the cliff about 1,000 m from sea where they fed. The jaegers nested in a loose aggregation on the moorland above the cliff. There they held small territories within which they mated, nested, and fed to some extent on arthropods. However, they obtained major parts of their food by kleptoparasitism (Arnason and Grant 1977). The jaegers gathered in the airspace in front of the puffin cliff and patrolled among the incoming puffins. Upon locating a fish-carrier the jaegers chased the puffin and tried to force it to drop the fish. The puffin tried to avoid the jaegers. It often gained speed by descending and headed for safety at the cliff or else it turned back to sea. The jaegers were non-territorial at the cliff; presumably puffins flying at high speed and clumped in space and time (Grant 1971) were a non-defendable resource (Brown 1964).

The light phase was the rarer morph in my study area (9.7% on the south coast of Iceland, Bengtson and Owen 1973). During chases involving a single jaeger the light-phased ones induced puffins to drop their fish in 81% of the chases whereas the dark-phased ones did so in 63% of the chases (Table 1). This difference is significant ($t = 2.21$, $P = 0.014$, one-tailed test of equality of percentages, Sokal and Rohlf 1969: 608). After a jaeger had 'surprised' a puffin and initiated a chase it was frequently joined by other jaegers. A pair of a light and a dark jaeger was significantly more successful in inducing puffins to drop the fish than was a pair of dark jaegers (Table 1, $t = 1.82$, $P = 0.034$, one-tailed test). The mixed chases are likely to have been initiated by a light bird half of the time. These results therefore accord well with the success of the chases of single jaegers. In the larger groups (3–6) differences in the same direction were found between the success of the all dark groups and the mixed groups (Table 1), although statistical significance was not found ($t = 0.79$, $P = 0.215$, one-tailed test), perhaps due to the small sample sizes.

Thus in this study area individuals of the rarer morph (light phase in this case) appeared to have greater hunting success than the more common ones, in agreement with the expectations of apostatic selection. However, when testing the apostatic selection hypothesis in field situations the success of the rare morph will always be determined by a relatively small number of observations. The observations may therefore represent only one or a few individuals that happen to be particularly skillful hunters compared to the average of both the common and the rare morphs. It is therefore important to know how many different individuals are involved. Three distinct light-phased types of Parasitic Jaegers are recognizable in the field: (1) with a light breast and belly, (2) with a narrow dark band across the breast, and (3) with a broad dark band across the breast. Individuals of all three types were regularly seen at the cliff chasing puffins. I surveyed the area close to the puffin cliff for breeding pairs and found 12 light-phased individuals at nine nests and 35 dark-phased individuals at 22 nests. All of these probably hunted at the puffin cliff. Throughout the puffin-jaeger interaction period, and at different times of the day, I censused the numbers of jaegers patroling in a fixed volume of air at the puffin cliff (Arnason and Grant 1977). When present there were 1–3 (average = 1.3 ± 0.5 SD, N = 21) light-phased individuals seen at the cliff at any one time, whereas there were 3–20 dark-phased individuals per census (average = 7.1 ± 3.1 SD, N = 28). Thus the data in Table 1 represent no fewer than three and perhaps as many as 12 different light-phased individuals and as many 20 to 35 dark-phased individuals.

An average puffin encounters a jaeger approximately twice a week and loses its fish approximately once a week (Arnason and Grant 1977). Thus the puffins have ample reinforcement for learning a "parasite image." Approximately nine out of every 10 chases involve only dark-phased jaegers and the reinforcement for learning to recognize the dark phase as a threat is thus much greater than for the light phase.

The Parasitic Jaeger is best characterized as a maritime species (Pitelka et al. 1955) holding mating, nesting, and partly feeding territories in loose aggregations close to the sea. It obtains major parts of its food by kleptoparasitizing seabirds nesting close by (Arnason and Grant 1977). These resources are probably economically undefendable (Brown 1964) and the jaegers are not territorial on their kleptoparasitic feeding grounds. Parasitic Jaegers are important predators of eggs and young of the Pink-footed Goose (*Anser brachyrhyncos*), which nests in the interior of Iceland. There the jaegers apparently also do not hold typical all-purpose territories, but rather hunt in groups of 2–3 on communal hunting grounds (Sigurdsson 1974 and pers. comm., and see Maher 1974). Thus the two major problems of applying the hypothesis of apostatic selection to predators are alleviated in the case of the Parasitic Jaeger. On the other hand, the Pomarine and Long-tailed Jaegers (*S. pomarinus* and *S. longicaudus*), the former likewise polymorphic, have typical all-purpose territories (Pitelka et al. 1955), feeding mostly on rodents (Maher 1974, Anderson 1976b) within their territories. Apostatic selection is unlikely under these circumstances, as noted above. However, all three species of jaegers are kleptoparasites on their wintering grounds at sea and apostatic selection may play a role during winter.

If apostatic selection was the sole factor affecting the frequencies of two morphs one would expect to find a stable equilibrium at 0.5. Deviation of the equilibrium frequency from 0.5 would depend on the genetic system of the predator and the perceptual abilities of the prey (i.e. the relative ease with which the prey forms an image of the two morphs, c.f. Clarke 1964), as well as on the presence of frequency-independent selective forces affecting the system (Clarke and O'Donald 1964), such as those proposed by O'Donald and Davis (1975, and see also Anderson 1976a on suggestions of aggressive camouflage in jaegers). If the morph frequencies have reached equilibrium locally (wherever it may be), theoretical models predict that the two morphs should be equally successful at the point of balance. However, in nature populations are finite and randomly drift away from the equilibrium. This creates selection back to the point of balance (the drift load, Kimura and Ohta 1971). Furthermore, the equilibrium gene frequencies may differ from the optimum phenotypic frequencies at which the fitness of the individuals is maximal (the dysmetric load, Kimura and Ohta 1971), creating additional selection. Clarke and O'Donald (1964) and Clarke (1964) have also shown that the presence of frequency-independent selective forces can lead to differential fitness at equilibrium. For these reasons we can expect selection to be operating most of the time. Proximately, we should therefore be able to measure differential hunting success of the two morphs at any locality and at any point in time, as was noted here for the Parasitic Jaeger.

The present observations accord with the prediction from the apostatic selection hypothesis. However, more data are needed to actually test the hypothesis. Data on the feeding efficiency of the two morphs of jaegers and avoidance responses of the puffins are needed from different populations from various parts of the jaegers' range. I therefore make a plea to Scandinavian workers to provide data from areas where the dark morph is rare and should be at an advantage, and to British workers, where the light-phased birds are rare and should be at a greater advantage than reported here, if apostatic selection indeed operates on the Parasitic Jaeger.

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ERRATA

The Proceedings of the 95th Stated Meeting of the American Ornithologists' Union [Auk 95 (1, Suppl.)] contains a resolution (number 7, page 11AA) considered by the Council but not presented to the General Session for adoption (see p. 5AA). Copies of those Resolutions adopted at the 95th Stated Meeting of the A.O.U. are available from the Secretary.

The caption for Table 1 in the article "Effect of cowbird parasitism on American Goldfinch nesting" (Auk 94: 304–307) is incorrect. The correct caption should read: "Comparison between clutch size and nesting success of parasitized vs. unparasitized and *un*parasitized adult goldfinches." Likewise, in columns 3 and 4, reference in both cases is to *un*parasitized nests.

ONTOGENY OF VOCALIZATION IN THE GREATER RHEA

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ABSTRACT.—The call-notes of the Greater Rhea chick were classified according to their acoustical structure and behavioral context. Both rate of vocalization and tonal quality of call-notes were found to deteriorate as a function of maturation. Call-note production was completely eliminated by 7 weeks of age. Greater Rhea adults are silent except for such relatively infrequent vocalizations as "hissing" that sometimes accompanies agonistic behavior and a disyllabic "grunt" that only the male produces as part of a courtship display. Tracheal growth and a marked reduction in the intrusion of the internal tympanic membranes into the bronchial passages could contribute to the deterioration of vocalization. The use of vocalization as the primary channel of communication is replaced by visual display in the adults. These modalities are best suited to the ecological contingencies facing the chick and adult, respectively. *Received 17 March 1977, accepted 24 September 1977.*

A great deal of ornithological literature has focused on the vocal displays of birds (e.g. Thorpe 1961, Hinde 1969, Armstrong 1973). The attention accorded to bird vocalization is no doubt largely due to its central importance in avian social interaction. The suborder oscines of the passerine birds have been the most popular species for research in bird vocalization. There has been little interest in the vocalizations of nonoscines in general and ratite birds in particular. This is probably because the vocal repertoire of adult ratites is not very impressive. The Greater Rhea (*Rhea americana*), a large, flightless ratite native to the pampas of Argentina, is especially unimpressive. In the adult, vocal production is restricted to "hissing" during agonistic encounters and the disyllabic "grunt" of a sexually aroused male. In contrast to adults, Greater Rhea chicks are highly vocal. This is unlike most other species of birds whose vocal repertoires increase in complexity as a function of development. The ontogeny of vocalization in the Greater Rhea is a curious example of behavioral regression and may pose questions for theoretical treatments of behavioral ontogeny that treat it as a cumulative and progressive process.

METHODS

Eggs were laid by the Greater Rheas maintained at the Chicago Zoological Park, Brookfield, Illinois and incubated at the University of Chicago. A total of 33 chicks was hatched over 2 years, of which 20 survived past 2 months of age. Chicks were housed at the University of Chicago in a 0.9 × 1.2 m pen until 4 weeks of age, at which time they were transferred to a 90 m^2 outdoor enclosure at the Chicago Zoological Park.

Vocal behavior was recorded on a SONY tape recorder model TC-92. Over 20 h of vocalizations were recorded and are available upon request to the author. Sonagrams were made on a Kay Elemetrics, Co. audio spectrum analyzer model 6061 B. Vocal amplitude was determined by a linear scale sound level meter placed at a distance of approximately 1 m from the chick. Recordings were made daily at random times for the first 4 weeks of life. Additional recordings were also made on an intermittent basis between ages 4–8 weeks.

CALL-NOTE CATALOGUE

Several authors, from Hudson (1903) to Bruning (1973a), have used the phrase "plaintive cry" to describe a frequently heard call of the Greater Rhea chick. Bruning

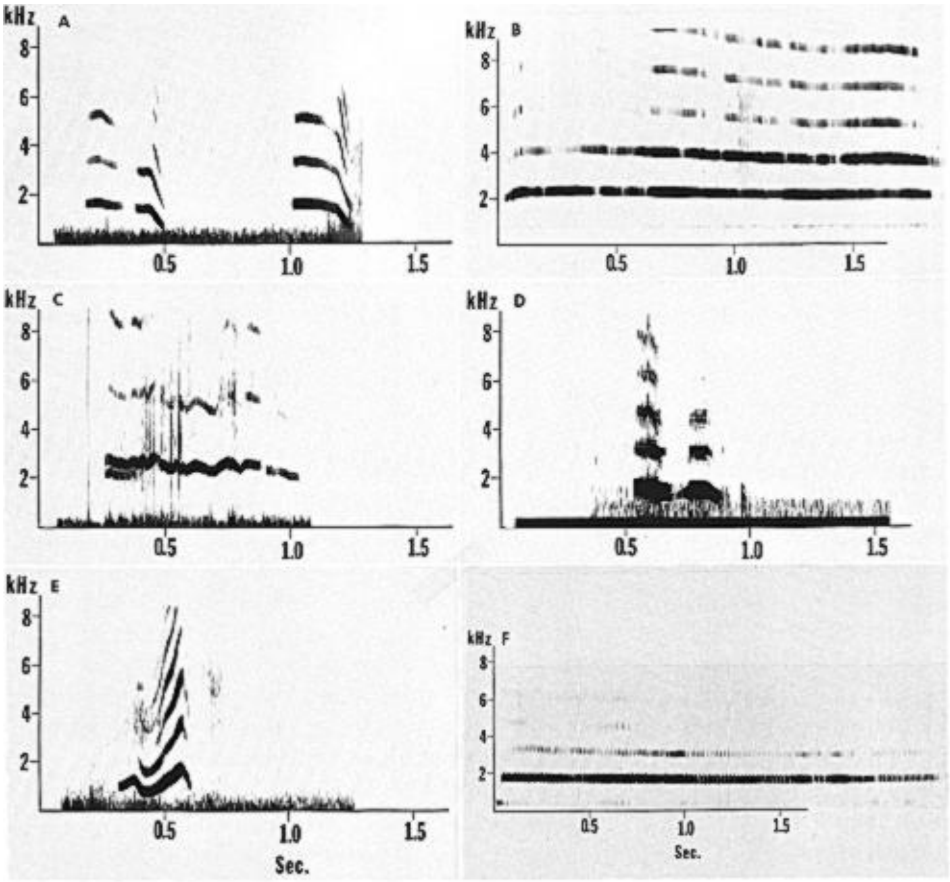

Fig. 1. Type B/65 wide-band sonagrams of Greater Rhea chick call-notes: (a) contact-whistle, (b) separation-whistle, (c) alarm-trill, (d) feeding-peep, (e) contentment-chirp, (f) separation-whistle of an older chick illustrating tonal deterioration.

also makes reference to an infrequently heard alarm cry produced when the chick was in immediate danger. Beyond these observations no one has made a detailed catalogue of Greater Rhea chick call-notes.

Based on observations of captive chicks in a variety of experimental conditions, five call-notes (Fig. 1) were detected and investigated. The call-notes were supplied with terms that reflect both their function and sound: (1) contact-whistle; (2) separation-whistle; (3) alarm-trill; (4) feeding-peep; and (5) contentment-chirp.

Contact-whistle.—The contact-whistle call-note sounds much like a soft, short whistle. It is a brief, monosyllabic call-note, with a duration of 0.20–0.50 s. It is also of relatively low amplitude, rarely exceeding 75 db. The fundamental frequency is generally around 1.5–2.0 kHz. There are several harmonics, at about 2.0 kHz intervals, which reflect the brilliance of the tone. Some chicks have a sharp decrease in pitch at the end of the note, while others exhibit a sharp decrease at the beginning of the note; with others there are no sudden changes in pitch. These variations appear to be specific to individuals.

The contact-whistle call-note was initially heard after the Greater Rhea embryo entered the air space (determined by candling), generally 2–5 days prior to hatching. The contact-whistle was emitted spontaneously by the embryo. It was also elicited on several occasions in response to the tape recorded playback of this call as well as to such mild stimulation as the slow turning of the egg. Such in-egg vocal production may act to synchronize the hatching of Greater Rhea eggs that are incubated together in a clutch. Pilot research by Bruning (1973b) indicated spectacular hatching synchrony, accelerating the time to hatching of late set eggs by as much as 7 days. In-egg vocal behavior in other species may be a potential variable in hatching synchrony (Orcutt 1974).

The contact-whistle remains very prominent in the repertoire of the Greater Rhea chick after hatching. It was frequently emitted in the presence of a human surrogate parent, especially when the chick was following or approaching. It was also frequently emitted in the presence of conspecifics with which the chick was reared. Since the call-note is heard only in these situations I suggest that it serves a social contact function.

Separation-whistle.—The separation-whistle call-note sounds much like a loud, long whistle. This call-note is the "plaintive cry" documented by Hudson (1903) and Bruning (1973a). It is a long, monosyllabic call-note, generally lasting 1.0–3.0s. The longest separation-whistle recorded was 4.48 s. The separation-whistle is a high amplitude call-note, reaching 75–100 db. The fundamental frequency is generally around 2.0 kHz. There are several harmonics, at about 2.0 kHz intervals, which reflect the brilliant tonal quality of the call-note. There are several individual-specific variations in pitch changes during separation-whistles. Some variations involve a sudden or gradual frequency decrease, which intensifies the sad or lonely quality of the call-note to the human ear. The fundamental remains level for some chicks while for others it gradually decreases, by 0.1–1.0 kHz, over 1–3 s. Some chicks show a sudden decrease in frequency at the onset of the call-note, while others show a sudden increase, but most chicks have neither. Some chicks show a sudden decrease in frequency at the tail of the call-note while others do not.

The separation-whistle is first heard within a few hours after hatching. The separation-whistle appears to be functionally related to the contact-whistle. Whereas the contact-whistle is emitted when the surrogate parent or familiar conspecifics are nearby, the separation-whistle is emitted in a condition of social isolation or when with unfamiliar conspecifics. The separation-whistle also appears to be acoustically related to the contact-whistle; its distinction is that it is longer and louder. There is no clear border between the two call-notes. If the surrogate parent is gradually displaced to some distance but the chick retains visual contact, the contact-whistle escalates in both duration and amplitude, gradually assuming the character of a separation-whistle. The inter-individual variations in pitch at the termination of the contact-whistle reflect those of the separation-whistle, again suggesting a close relationship between the two call-notes.

Alarm-trill.—The alarm-trill call-note has many acoustical features in common with the separation-whistle. It is a long, loud monosyllabic call-note. The duration is generally somewhat shorter than that of the separation-whistle, lasting 0.5–2.0 s. The amplitude measures 80–90 db. The fundamental frequency is generally around 2.0 kHz. There are several harmonics, at about 2.0 kHz intervals. The distinguishing feature of the alarm-trill is a modulation of pitch throughout the call-note.

The alarm-trill is elicited by stressing the chick with such procedures as suddenly lifting it off the ground or by administering intra-muscular injections of medicine or vitamin supplement. The alarm-trill is not heard from all chicks as some consistently remain silent throughout these procedures.

The alarm-trill is acoustically similar and seems to be functionally related to the separation-whistle. Both probably function to attract the parent to the chick. But the modulation of pitch in the alarm-trill may serve to give it somewhat greater emphasis or urgency than the separation-whistle.

Feeding-peep.—The feeding-peep is a very quiet, short, monosyllabic call-note. From one to four feeding-peeps are generally emitted in rapid succession. The duration of a single feeding-peep is usually 0.15–0.20 s. The amplitude was not detectable above the ambient noise level of 60 db. The fundamental frequency is 1.0–1.5 kHz, slightly lower than that of the other call-notes. There are several harmonics at about 1.5 kHz intervals. No inter-individual variations were detected.

The feeding-peep is first heard shortly after the chick began to feed. Thereafter it is commonly heard during feeding. It is not heard in any other behavioral context.

Contentment-chirp.—The contentment-chirp is a short, monosyllabic call-note. Its duration was brief but more variable than that of the feeding-peep, lasting 0.10–0.35 s. Its amplitude measures 70–75 db. The contentment-chirp is characterized by sharply rising pitch. The fundamental frequency is generally low, starting at 0.5–1.0 kHz and rising 1.5–2.0 kHz. There are several harmonics, spaced at about 1.0 kHz intervals. There seemed to be individual-specific variations in the acoustical structure, such as the presence or absence of slight dips in pitch at the beginning or end of the call-note, but not enough recordings were made to permit detailed analysis.

The contentment-chirp is an infrequently heard vocalization that was recorded from one to only a few times in most of the chicks. The call-note was not reliably elicited with any condition. It was sometimes produced when the chick was reunited with the surrogate parent or a familiar conspecific after a period of isolation and was also occasionally heard when a chick found food.

VOCAL DECLINE

The most unusual aspect of vocalization in the Greater Rhea is its deterioration during ontogeny. Greater Rhea chicks have a variety of call-notes of brilliant tonal quality that are frequently emitted. But by the time they are adults they are relatively silent. Such a regression in vocal behavior deviates considerably from most species of birds in which the complexity of vocalization increases as a function of maturation.

The rate of vocalization was found to decrease steadily with age (Fig. 2). The rates of vocalization of three call-notes, the contact-whistle, the separation-whistle, and the feeding-peep, were determined during the second, fourth, and sixth weeks post-hatch. The contentment-chirp and alarm-trill were not included in the analysis since they are both relatively infrequent call-notes, not reliably elicited from all chicks. However, it appears that both of these call-notes share the general pattern of decline with increasing age. The rate of contact-whistles emitted in the presence of the surrogate parent decreased significantly as a function of age ($P < .001$, ANOCOVA). The rate of feeding-peeps emitted during feeding also decreased significantly with age ($P < .001$, ANOCOVA). Finally, the rate of separation-whistles elicited in a condition of isolation from the surrogate parent and conspecifics also decreased significantly with age ($P < .001$, ANOCOVA). The decline of vocalization rate for the separation-whistle was less severe; the regression coefficient for the separation-whistle rate was statistically different from the regression coefficients for

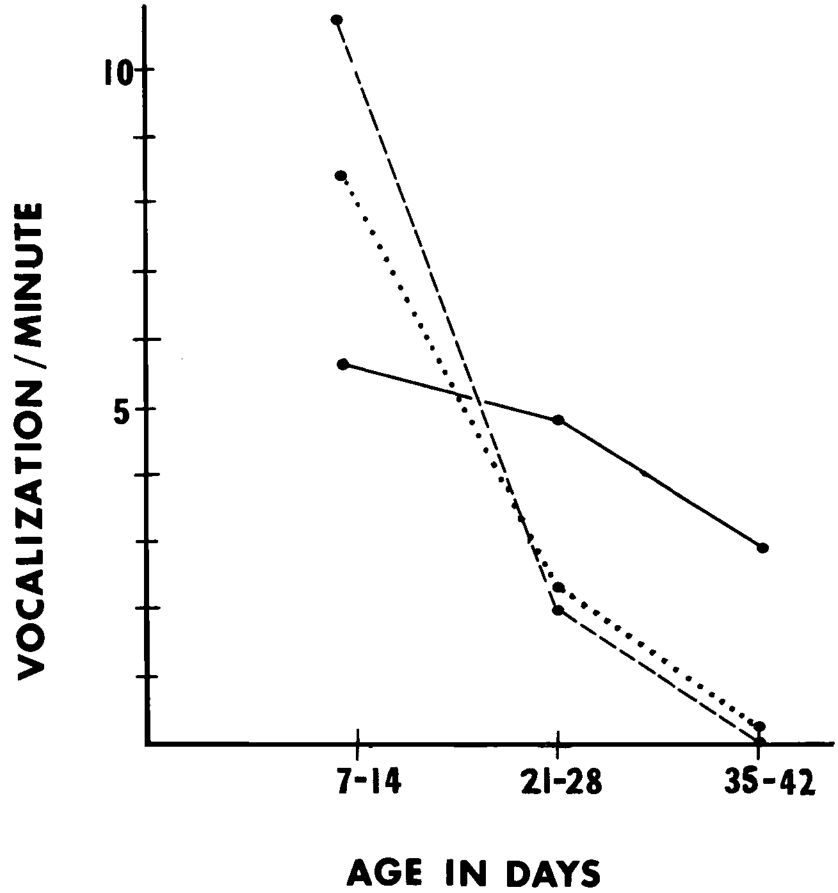

Fig. 2. The rate of vocal production as a function of age in Greater Rhea chicks. Dashed line = feeding-peep rate; dotted line = contact-whistle rate; solid line = separation-whistle rate.

the two other vocalization rates. This may reflect some extended functional significance of the separation-whistle. Only the separation-whistle call-note was still heard after 42 days of age. The oldest age at which a separation-whistle was elicited was 64 days. The call-note in this instance was very hoarse and feeble.

In addition to the decline in the rate of vocalization, there is also a deterioration in tonal quality. Changes first become evident after 17 days post-hatch. Instead of being sharp or even shrill-sounding, the call-notes sound increasingly hoarse. Call-notes showed a decrease in the number of harmonics with age (Fig. 1F). Long call-notes such as the separation-whistle or alarm-trill often had breaks in the production of a single note whereas it was smooth and continuous in younger chicks. This resulted in a choppy and gutteral sound. The amplitude of the call-notes also decreased steadily past 17 days of age.

ANATOMY

Two chicks, aged 11 and 15 days, and a 1 yr old adult female Greater Rhea, all of which had died of illness, were used for a pilot investigation into the anatomical basis of vocalization. The resonant frequencies of vocal production are known to depend

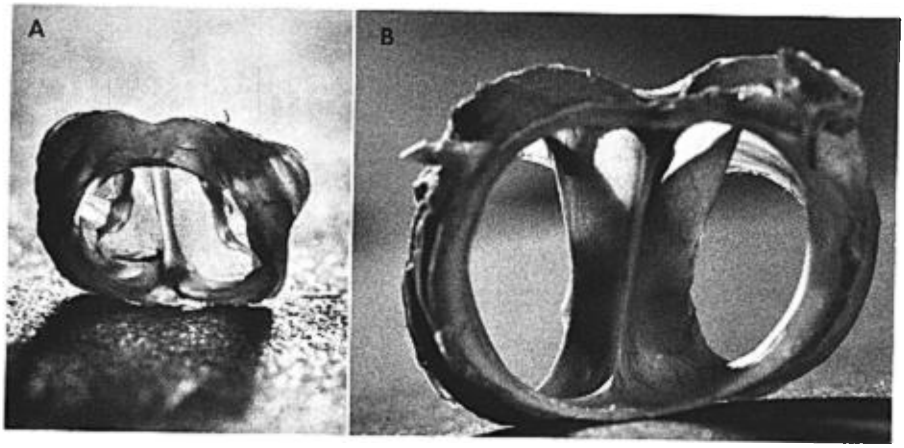

Fig. 3. **Internal syrinx. Left: a cross section from an 11-day-old chick; the diameter measures approximately 0.5 cm. Right: a cross section from a 1-yr-old; the diameter measures approximately 2.0 cm. Note the reduction in the intrusion of the tympanic membranes into the bronchial passages.**

on the length and diameter of the trachea. The lengths of the chicks' tracheas were 12 and 13 cm, and the diameter in both cases was approximately 0.5 cm. The length of the adult's trachea was 42 cm and its diameter varied from 2.5 cm measured just below the larynx to 2.0 cm measured just above the syrinx. Greater Rhea chicks lose their vocal ability when they reach approximately one-third of their adult height. Perhaps the growth of the trachea is a contributing factor.

A cross section incision was made through the trachea just above the syrinx, allowing for an excellent view of the internal tympanum. The tympanum is thought to be the primary source of vibration and thus the major anatomical structure in avian vocalization (Greenewalt 1968). The tympanum vibrates as air is forced past the internal membranes which are stretched into the bronchial passages at the point of entry into the trachea. In the Greater Rhea, the internal tympanic membranes intruded into the bronchial passages to a much greater extent in the chicks than in the adult (Fig. 3). The internal tympanic membranes of the adult do not seem capable of closing the air passages to the extent necessary to produce the resonance of the chick call-notes.

ECOLOGY

Levins (1968) postulated that one adaptive strategy to deal with predictable changes in ecological contingencies, such as seasonal variations, is a modification of the phenotype correspondent to the ecological parameter. Ontogeny often poses an analogous problem to an animal. The ecological contingencies that confront an animal in its infancy may be quite dissimilar from those it faces in adulthood. A consideration of this process may account for the regressive nature of vocal ontogeny in the Greater Rhea.

The vocal channel of communication seems well adapted to the ecological contingencies that confront the Greater Rhea chick. Chicks suffer greatly from predation by the Crested Caracara (*Polyborus plancus*) as well as other avian and mammalian predators. These predators rely primarily on visual cues in obtaining prey. Aided by its cryptic coloration, the Greater Rhea chick may reduce the probability of predator detection by blending in with the tall grass of its native Argentine pampas. However, the resulting low visual profile of the chick may also increase the probability that the parent will lose visual contact with the young. Given this situation, the vocal channel seems to be the optimal method of communication for the chicks. The variety of chick call-notes seem well suited to maintain contact with the parent and to signal when the chick is lost, in danger, or feeding.

Between 6 to 10 weeks of age seems the turning point in vocal behavior and ecology. At this time chicks lose their vocal prowess, lose the cryptic coloration provided by the neossoptiles, and begin to outgrow the protective cover offered by tall grass. They are also probably too large at this age to suffer heavily from predation by the Crested Caracara. In Greater Rhea juveniles ritualized visual displays are elaborated for social communication. Descriptions of some of the adult visual displays have been provided by Raikow (1969) and Bruning (1975). The visual channel of communication seems well suited to the ecological contingencies of adults, which do not suffer from natural predators. They are also large-bodied animals, attaining a height of 1.5 m, and are not cryptically colored. They therefore stand out noticeably from the surrounding flat, grassland habitat. Visual display would seem to be the most efficient method of communication in this situation.

ACKNOWLEDGMENTS

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DIFFERENTIAL RESPONSE OF TERRITORIAL YELLOWTHROATS TO THE SONGS OF NEIGHBORS AND NON-NEIGHBORS

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ABSTRACT.—Songs of neighbor and non-neighboring individual Yellowthroats were presented to territorial male Yellowthroats in two different locations within the territory. Territorial males showed a significantly higher aggressive response to the songs of strangers than neighbors when the speaker was placed near the respective neighbor's boundary. Presentation of the two songs in the center of a territory resulted in a high aggressive response to both songs, with no discernable difference in response. Evidence is also presented that suggests that females are capable of recognizing their mates by song alone. *Received 13 October 1976, accepted 28 December 1976.*

THE importance of individual recognition in the efficiency and success of colonial bird species has been emphasized by Thorpe (1961) and Beer (1970) as well as others. Even within noncolonial species, individual recognition has been demonstrated and probably is helpful in pair bond maintenance as well as in the efficient maintenance of the territory. Birds that sing antiphonally, e.g. the *Laniarius* shrikes (Grimes 1966, Hooker and Hooker 1969), recognize their mates by song alone. Certain cardueline finches learn their mate's call by imitation (Mundinger 1970). The ability to discriminate between the songs of neighboring males and those of non-neighbors was demonstrated in the Ovenbird, *Seiurus aurocapillus* (Weeden and Falls 1959), Great Tit, *Parus major* (Gompertz 1961, Krebs 1971), White-throated Sparrow, *Zonotrichia albicollis* (Falls 1969), Indigo Bunting, *Passerina cyanea* (Emlen 1971), Field Sparrow, *Spizella pusilla* (Goldman 1973) and the Song Sparrow, *Melospiza melodia* (Kroodsma 1976) by the use of song playback.

Yellowthroats (*Geothlypis trichas*) are a widespread species commonly found breeding in early seral stages of succession throughout North America. Their territories are in brushy areas and males are rarely in visual contact with neighboring males or with their own mates. It seems unlikely that visual cues are helpful in supplying much contextual information to the song which might expand the number of potential meanings of messages transmitted (cf. Smith 1965). Although visual cues might be important at close range, vocal cues are probably particularly critical in the transmission of information pertaining to an individual's sex, species, motivational state, and the singer's own identity.

The advertisement song of the Yellowthroat is commonly paraphrased as "wich-i-ty wich-i-ty wich-i-ty." Each male sings only one primary song that does not change (Wunderle, unpublished data). Song variation within the individual's repertoire is slight while the variation between the songs of different individuals is great (Borror 1967). The variation within note structure and number of notes per phrase probably provides ample information for individual recognition. The objective of this study was to determine if male Yellowthroats can discriminate between the songs of neighbors and strangers, and to examine the role of song source position within a territory.

The Auk 95: 389–395. April 1978

METHODS

During June of 1972 and 1973, playback experiments were run on male Yellowthroats at the Kalbfleisch Field Research Station of the American Museum of Natural History, in Dix Hills, Long Island, New York. In both years territories were mapped by observing singing males and delineating territorial boundaries by use of playback. Each experiment was run approximately 1 week after the territory was mapped. During all playback presentations an Electravoice speaker was placed upright on the ground and was attached to a 7.6-m cable connected to an amplifier and a Uher 4000 Report-L tape recorder. No models or mounts of male birds were used. In the summer of 1972, the speaker was placed in the center of known territories and eight individuals, seven of which were color-banded, were tested. In the summer of 1973 the same speaker was placed at the edge of known territories, where the territory abutted with that of a neighbor. Seven color-banded and one unbanded individual were tested in that configuration.

To test a bird's ability to discriminate between the songs of neighbors and strangers, recordings were made of adjoining neighbors and two individuals located approximately 19.3 km away. It is likely that the test individuals had no previous experience with the two songs of the more distant males. Three-min tapes were made of neighbors and non-neighboring Yellowthroats with songs spaced at 15-s intervals, an interval characteristic of an undisturbed singing bout. All birds were recorded with a Uher 4000 Report-L tape recorder at 19 cm per s using a 61-cm parabolic reflecter with a Uher microphone.

The two songs of the distant males differed from the songs of neighbors in both note morphology and number of notes per repeated phrase. Kalbfleisch males sang songs with three-note repeated phrases, while the songs of the two strangers were made of four-note repeated phrases.

Songs of a neighboring or a non-neighboring male were presented to individuals in random order, with a 15-min interval between the playing of each tape. Prior to each tape presentation, an 8-min period was used to observe and record the behavior of the undisturbed male. Then during the 3-min tape presentation and the following 5 min all behavior was again recorded. The 8-min control period was used as a baseline with which the combined responses obtained from the tape presentation period and the following response observation period were compared. The difference between the control period and the tape period with its associated observation period was calculated for the number of occurrences of each specific behavior as listed in the behavioral index (Table 1). It was this difference (tape response period and following 5 min minus the control count period) that was used to calculate the behavioral index.

Observations of numerous territorial interactions of male Yellowthroats permitted me to calibrate a behavioral scale as used by Emlen (1971). The most reliable technique for measuring response level seemed to be a hybrid index (Sibley 1954) as adapted for behavioral purposes by Emlen (1971). I concluded that the most reliable indication of a highly excited male is the appearance of numerous types of vocalizations, flights over the speaker, and approaches to the speaker. Normally, a strange male singing near the boundary of a territorial resident male would stimulate an increase in singing by the territorial male. Following the increased singing rate, the territorial male would chatter several times before actually approaching and chasing the intruder. The chatter vocalization is made up of a series of rapidly uttered notes having a rattling-chattering quality which was heard only during territorial encounters. If the intruder did not immediately leave the territory, the territorial male might again sing, or more likely, chatter before attacking and chasing again. Several single high-pitched notes (designated as "chit" notes) were often given between singing, chattering and chasing. The behavioral response index (Table 1) lists those behavioral responses that were recorded during playback experiments.

A comparison of the behavioral response index score of the neighbor's song with the stranger's song was made with the Wilcoxon Matched-Pairs Sign-Rank test (Siegel 1956). A two-tailed test was used because the experimental results were not predictable in advance. The Mann-Whitney U-test was used to compare specific behavioral changes between the two songs.

RESULTS

A comparison of the response to the song of a neighbor and of a non-neighbor when the speaker is placed along the respective neighbor's shared boundary (Fig. 1) indicates a significant difference ($P < .01$) in response. Males show a higher response to the song of strangers than to the song of neighbors when the speaker is placed along the mutual boundary. A comparison of the individual response behaviors, i.e. increase in primary song, increase in chit notes, chatters, flights over the speaker, and number of speaker approaches shows a significant difference ($P < .05$). Table 2

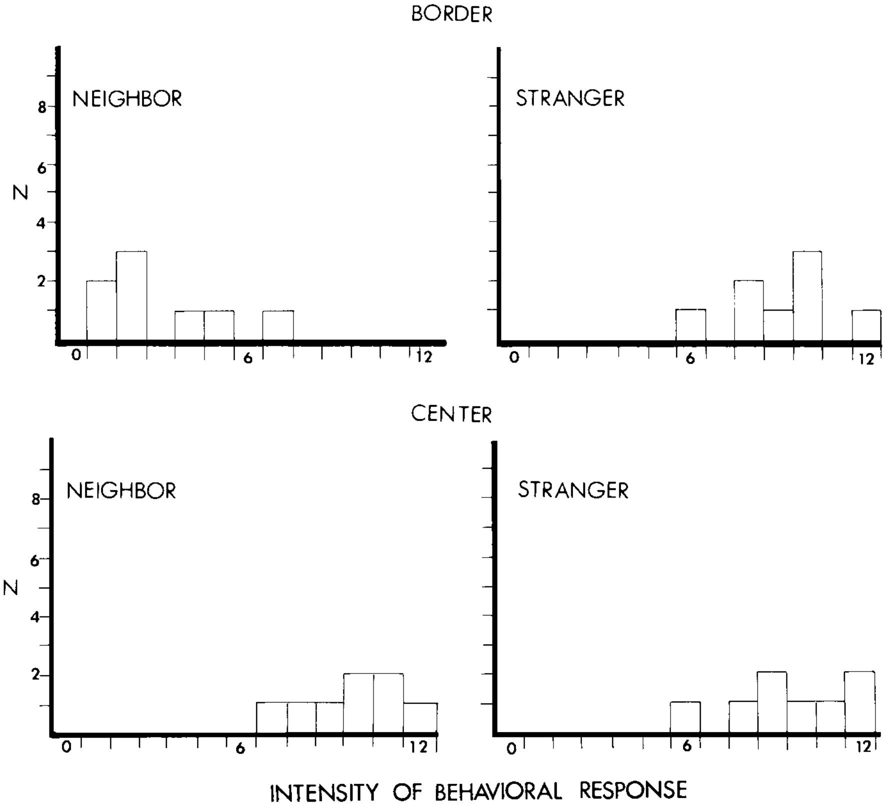

Fig. 1. Responses of male Yellowthroats to the songs of neighbors and strangers when the speaker was placed near the mutual boundary (above) and when the speaker was placed in the center of the territory (below). N = number of birds tested.

displays the average number of responses for each particular behavior elicited by the two different songs. When the speaker was placed in the middle of the territory, however, the resident male responded equally and with high intensity to songs of both neighbors and strangers (Fig. 1, Table 2).

DISCUSSION

These results suggest that male Yellowthroats discriminate between the songs of neighbors and non-neighbors when the speaker is placed near the neighbor's boundary, but presentation of the two different songs in the center of a territory elicited a highly aggressive response to both. Thus male Yellowthroats are capable of discriminating between songs, yet a response indicating such discrimination is dependent upon the location of the singer.

The differential agonistic responses of territorial males elicited by familiar and unfamiliar songs presented along the neighboring male's territorial boundary suggest that the male has habituated to both his neighbor's song and physical location. The occurrence of only one song per male and the existence of many different song types within a Yellowthroat population probably enhance individual recognition. Any change in either the neighbor's song or singing location disrupts the status quo to

TABLE 1. Behavioral response index used to quantify a male's response to playback. Six categories of behavioral activity were used for comparing both the control count period (8 min) with the playback plus response observation periods (8 min total). A score of 0, 1, or 2 for each category indicated no change, slight increase, and large increase, respectively, during playback and following 5 min compared to the control count observation periods. N = number of occurrences of the specific behavior per experiment

Singing rate (songs per 8 min)
  0 = No change or decrease
  1 = Rate increase $2 \leqslant N \leqslant 6$
  2 = Rate increase $N \geqslant 7$

Chit notes (*chit* notes per 8 min)
  0 = No change or decrease
  1 = Increase $1 \leqslant N \leqslant 3$
  2 = Increase $N > 3$

Chattering (chatters per 8 min)
  0 = No change or decrease
  1 = Increase $1 \leqslant N \leqslant 2$
  2 = Increase $N > 3$

Flights over the speaker (in 8 min)
  0 = No change or decrease
  1 = Increase $1 \leqslant N \leqslant 2$
  2 = Increase $N > 2$

Approach distance
  0 = None
  1 = $3\text{ m} \geqslant N \geqslant 1.5\text{ m}$
  2 = $N < 1.5\text{ m}$

Number of approaches within 3 m
  0 = None
  1 = $1 \leqslant N \leqslant 3$
  2 = $N > 3$

Maximum Possible Score = 12

which the male has habituated. Weeden and Falls (1959) suggested that habituation to the songs of established neighbors results in a considerable saving of energy for the territorial male by reducing the number of "needless" boundary conflicts. Habituation appears to be an important mechanism for maintaining low levels of aggression between neighboring conspecifics (Petrinovich and Peeke 1973).

Where time and energy might be conserved by not responding to a neighbor's song in a familiar location, the occurrence of the neighbor's song in an unexpected site demands an immediate response by the territorial male. The song of an intruder within the center of a territory represents an immediate threat to the territory of the resident male, regardless of the singer's identity.

The song of an unfamiliar male elicited a highly aggressive response, regardless of location. Such an unfamiliar song might represent the song of nonterritorial males, possibly members of a floating population that are constantly attempting to carve out a new territory, often from pre-existing ones (Wunderle, unpublished data). An aggressive response to such unfamiliar males is clearly adaptive.

TABLE 2. A summary of the individual response parameters elicited by playback of the songs of neighboring and non-neighboring males. Eight different males were tested at each speaker location

	Average Number of Various Response Parameters				
	Primary Song	Chit Notes	Chatter	Flights	Approaches[a]
Speaker near the mutual border					
Prior to playback	2.4	0.1	0	0	0
Playback, Non-neighbor song	8.1	2.9	4.5	2.1	0.4
Prior to playback	3.6	0.8	8	8	8
Playback, Neighbor song	1.6	1.0	0.9	.13	2.5
Speaker in center of territory					
Prior to playback	2.1	0	0	0	0
Playback, Non-neighbor song	8.2	3.1	5.1	4.0	4.1
Prior to playback	1.8	0.1	0	0	0
Playback, Neighbor song	8.0	2.9	5.7	4.3	3.9

[a] Refers to the number of approaches to within a 1.5-m radius of speaker

The experimental evidence presented for the Ovenbird (Weeden and Falls 1959), Indigo Bunting (Emlen 1971), and Great Tit (Gompertz 1961, Krebs 1971), in which the speaker was placed in only one location in a territory, does not necessarily indicate that a male can recognize a particular individual by voice alone. As pointed out by Beer (1970: 39), these types of experiments indicate only that a territorial male is capable of differentiating between classes of familiar and unfamiliar songs. Individual recognition by voice cannot be assumed under these circumstances because the bird is responding in a differential fashion to familiar and unfamiliar songs. Playback experiments comparing the response to songs of neighbors and non-neighbors done in only one location in a territory should be designated only as neighbor/non-neighbor discrimination experiments and not as tests of individual recognition. For the efficient maintenance of territoriality it is not necessary to assume that males are capable of individual recognition, but that they can discriminate between the songs of neighbors and strangers (Beer, op. cit.). A male's ability to associate familiar songs with a given location would permit the most efficient territorial defense.

Brooks and Falls (1975) demonstrated that male White-throated Sparrows could differentiate between the songs of neighbors and strangers. In addition, Falls and Brooks (1975) showed that a particular male responded differentially to the song of a given neighbor depending upon the location in which the speaker was placed within the territory. A song of a neighbor played along the mutual boundary elicited a weak response, whereas the rendition of the same song on the opposite boundary elicited a strong response from the territorial male. They essentially demonstrated that a territorial male could differentiate between the songs of neighbors A and B. Such methods, taking location differences of the speaker into consideration (contextual differences), offer strong evidence for individual recognition.

Failure to demonstrate neighbor and non-neighbor discrimination of song could be due to speaker location. Belcher and Thompson (1969) working with Indigo Buntings and Harris and Lemon (1976) working with Song Sparrows found that territorial males did not respond differently to the songs of neighbors and strangers. However, Emlen (1971) with Indigo Buntings and Kroodsma (1976) with Song Sparrows both found that males showed a stronger response to the songs of strangers than neighbors. Such discrepancies could result from differences in speaker location as well as the time in the breeding season when the experiments were run.

If songs are variable among males, and if males can recognize these differences, it seems likely that females could recognize their mates by song alone. During playback of Yellowthroat songs to territorial males, some females were occasionally heard giving the chatter call while their mate gave the normal aggressive response. From these observations it was not possible to determine if the female was responding aggressively to the stranger's song or if she was stimulated by her mate's aggressive response. However, during some preliminary playback experiments a resident color-banded male left his territory. Prior to his leaving he was actively singing and foraging with his mate. Upon his departure, playback of his own song to his visibly present mate elicited no response from her. However, playback of two other songs from unfamiliar males elicited several chatter calls, suggesting recognition of her mate by song alone.

To further test the possibility that females are capable of recognizing their mates by song alone, three different color-banded males were netted and removed from their territories. An hour after their removal, the song of an unfamiliar male and their own song were played in their respective territories. In two of the territories, females responded to the unfamiliar song with several (two and three) chatter calls and remained silent during the playback of their own male's song. The third female remained silent throughout and was not observed; possibly she was incubating at the time. Petrinovich et al. (1976) have demonstrated that a female's aggressive response to playback depends upon whether she has eggs, nestlings, or fledglings. The females that did respond were believed to be in the process of nest building or egg-laying. Such preliminary experiments suggest that females are capable of recognizing their mates by song alone.

Female Yellowthroats do not necessarily mate with the same male each year. I found that females may pair with a neighbor the next year, or may exchange mates in the course of a summer. The number of potential mates that a females might have during a lifetime suggests that she must have a flexible learning scheme if she is to recognize all of her mates individually by song.

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Increased use of computers to store and process data about birds has precipitated a number of problems. One such problem is that of identifying the species (or higher taxonomic unit) under consideration. Many local ornithological organizations have solved this problem by identifying each species in their area with a unique code number (AOU number, for example). The proliferation of local systems could be avoided by development of an internationally recognized coding system for all bird species. The advantages of a standard system include international compatibility of records and facilitation of exchange of data and literature between countries.

Any new system must be taxonomically based, flexible enough to accommodate new species and taxonomic revisions, and be expandable for those interested in subspecific classification. For purposes of discussion, the following system is proposed. A world-wide numerical system will be based on Morony, Bock and Farrand (Reference List of the Birds of the World, 1975, AMNH) with 6-digit numbers identifying each species: the first two digits key order, the third digit family, the fourth digit genus, and the final two digits the species. Thus, each genus has numbers reserved in advance for up to 99 species, and searches of data can be made rapidly and efficiently by computer for any taxonomic level. Individuals wanting subspecific identifications can simply add one or two digits to the 6-digit base.

As an example:

- 270000 Cuculiformes
  - 271000 Musophagidae
    - 271100 Corythaeola
      - 271101 *C. cristata*
    - 271200 Crinifer (2 spp.—201–202)
    - 271300 Corythaixoides (3 spp.—301–303)
    - 271400 Musophaga (2 spp.—401–402)
    - 271500 Tauraco (11 spp.—501–511)
  - 272000–279000 Cuculidae
- 280000 Strigiformes
- 290000 Caprimulgiformes

A conversion table from old numbers (AOU, etc.) to new numbers should be developed for study of zoological material, bird banding, and other references to old numbers. Interested persons are invited to send comments about this proposal to **James R. Karr, Department of Ecology, Ethology, and Evolution, University of Illinois, Champaign, Illinois 61820, U.S.A.**

A special discussion group at the International Ornithological Congress in Berlin will discuss this and other proposals and all comments received by **15 May 1978**. A final recommendation will then be developed and circulated to the international ornithological community for comment and eventual adoption.

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The **American Ornithologists' Union** will hold its **96th Stated Meeting** during the week of 14–18 August 1978 at the University of Wisconsin-Madison at the invitation of the Department of Wildlife Ecology and the Department of Zoology of the University of Wisconsin-Madison, the Wisconsin Society for Ornithology, and the Madison Audubon Society. A Circular of Information providing details of the meeting and a formal call for papers will be sent to the A.O.U. membership. Chairman of the Local Committee is Dr. Stanley A. Temple, Department of Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53706. Chairman of the Committee on Scientific Program is Dr. Ralph W. Schreiber, Natural History Museum, 900 Exposition Boulevard, Los Angeles, California 90007.

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George Lowery, a Past-President of the A.O.U., passed away on 19 January 1978. A **Lowery Memorial Fund** has been established to provide an endowment from which expenses of research and publication by the staff, students, and associates of the LSU Museum of Natural Science may derive support. Persons wishing to contribute to this fund may do so through the **LSU Foundation, 122 Systems Building, Louisiana State University, Baton Rouge, Louisiana 70803**. Indicate that contributions are intended for the Lowery Memorial Fund.

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The **North American Conference on Common Loon Research and Management**, sponsored by the National Audubon Society and hosted by Syracuse University, was held 12–14 August 1977 at the Minnowbrook Conference Center, Blue Mountain Lake, N.Y. Priorities determined by the participants included: (1) establishment of an informal working group to serve as a clearing-house for information on research and management efforts; (2) collection of historical loon nesting records for assessment of recent range contraction or expansion by this species; (3) coordination and standardization of breeding surveys and an effort to document the current breeding status of the loon, particularly in the northeastern U.S.; and (4) expanded research, including increased banding efforts and initiation of a winter banding program.

The working group, consisting of Judith W. McIntyre of Syracuse University, Richard L. Plunkett of the National Audubon Society, and Rawson L. Wood of the Loon Preservation Committee of the Audubon Society of New Hampshire, plans another meeting next year. Requests for conference summaries and other inquiries may be directed to the coordinator, **Judith W. McIntyre, Biology Department, Syracuse University, Syracuse, N.Y. 13210.**

The Linnaean Society of New York, as part of its centennial celebration, will host the Second Annual Meeting of the **Colonial Waterbird Group** at the American Museum of Natural History in New York City on **20–23 October 1978**. The Linnaean Society will sponsor a symposium of invited papers on factors affecting productivity in colonial species on 21 October and the morning of 22 October. Submitted papers will be given on the afternoon of 22 October and on 23 October. For information on contributing a paper, write to Dr. P. A. Buckley, **North Atlantic Regional Office, National Park Service, 15 State Street, Boston, Mass.** For registration information write to Miss Helen Hays, Department of Ornithology, American Museum of Natural History, Central Park West at 79 Street, New York, N.Y. 10024.

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Increased use of computers to store and process data about birds has precipitated a number of problems. One such problem is that of identifying the species (or higher taxonomic unit) under consideration. Many local ornithological organizations have solved this problem by identifying each species in their area with a unique code number (AOU number, for example). The proliferation of local systems could be avoided by development of an internationally recognized coding system for all bird species. The advantages of a standard system include international compatibility of records and facilitation of exchange of data and literature between countries.

Any new system must be taxonomically based, flexible enough to accommodate new species and taxonomic revisions, and be expandable for those interested in subspecific classification. For purposes of discussion, the following system is proposed. A world-wide numerical system will be based on Morony, Bock and Farrand (Reference List of the Birds of the World, 1975, AMNH) with 6-digit numbers identifying each species: the first two digits key order, the third digit family, the fourth digit genus, and the final two digits the species. Thus, each genus has numbers reserved in advance for up to 99 species, and searches of data can be made rapidly and efficiently by computer for any taxonomic level. Individuals wanting subspecific identifications can simply add one or two digits to the 6-digit base.

As an example:

- 270000 Cuculiformes
  - 271000 Musophagidae
    - 271100 Corythaeola
      - 271101 *C. cristata*
    - 271200 Crinifer (2 spp.—201–202)
    - 271300 Corythaixoides (3 spp.—301–303)
    - 271400 Musophaga (2 spp.—401–402)
    - 271500 Tauraco (11 spp.—501–511)
  - 272000–279000 Cuculidae
- 280000 Strigiformes
- 290000 Caprimulgiformes

A conversion table from old numbers (AOU, etc.) to new numbers should be developed for study of zoological material, bird banding, and other references to old numbers. Interested persons are invited to send comments about this proposal to **James R. Karr, Department of Ecology, Ethology, and Evolution, University of Illinois, Champaign, Illinois 61820, U.S.A.**

A special discussion group at the International Ornithological Congress in Berlin will discuss this and other proposals and all comments received by **15 May 1978**. A final recommendation will then be developed and circulated to the international ornithological community for comment and eventual adoption.