

AGE-RELATED DIFFERENCES IN RUDDY TURNSTONE FORAGING AND AGGRESSIVE BEHAVIOR

SARAH GROVES

ABSTRACT.—The foraging behavior of fall migrant Ruddy Turnstones was studied on the Massachusetts coast on 2 different substrates, barnacle-covered rocks and sand and weed-littered flats. Foraging rates differed significantly between the 2 substrates. On each substrate the foraging and success rates of adults and juveniles differed significantly while the frequencies of success were similar for both age-classes. The observed differences in foraging rates of adults and juveniles may be due to the degree of refinement of foraging techniques. Experience in searching for and handling prey may be a primary factor accounting for these differences, and foraging performance probably improves with age and experience. Alternatively, the differences may be due to the presence of inefficient juveniles that do not survive to adulthood.

Both adults and juveniles in the tail-depressed posture were dominant in aggressive interactions much more frequently than birds in the tail-level posture. In mixed flocks of foraging adult and juvenile turnstones, the four possible types of aggressive interactions occurred nonrandomly. Adult over juvenile interactions occurred more frequently than expected, and juvenile over adult interactions were never seen. A tentative explanation of this phenomenon may be that juveniles misinterpret or respond ambivalently to messages conveyed behaviorally by adults and thus become especially vulnerable to aggression by adults. The transiency of migrants made it unfeasible to evaluate the persistence of this nonrandom aggression.—*Manomet Bird Observatory, Manomet, Massachusetts 02345. Present address: Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 1W5, Canada. Accepted 13 July 1976.*

THE occurrence of higher mortality in young birds than in adults is widespread in avian species (Lack 1954). This markedly differential mortality in many species suggests that juveniles are somehow more inept than adults in coping with the rigors of survival. A variety of behavioral, social, and genetic factors may account for such differences.

Lack (1966) argues that food supply is the major factor in density-dependent population regulation, and Ashmole (1963) hypothesizes that starvation is a major factor in the higher juvenile mortality and implies that young birds are less efficient than adults in foraging. Foraging inefficiency can be attributed to a variety of behavioral differences including acquired proficiency and skill in searching for and handling prey (feeding rate, frequency of prey capture, size of prey selected, etc.) and those of a social or psychological nature related to aggression, dominance, flocking, and other social factors. To what extent these aspects of behavior interact to influence foraging efficiency is difficult to determine. Likewise the precise nature of behavioral differences may be ambiguous because of the difficulty of distinguishing between inherited, learned, and developed behaviors.

The purpose of this study was to examine differences, if any, in foraging and social behavior of conspecific juveniles and adults. Ruddy Turnstones (*Arenaria interpres*) were studied south of the breeding ground during southbound migration. Two aspects of behavior, foraging efficiency and the frequency of aggressive interactions between adults and juveniles were recorded in detail. Adults and juveniles were found to differ significantly in both these aspects.

STUDY AREA AND METHODS

Ruddy Turnstones were studied on the Massachusetts coast in Plymouth County, a region characterized by exposed ocean and estuarine beaches and extensive tidal flats. Turnstones were watched foraging on

different substrates including coarse pebbly and rocky beaches, wet firm sand close to the water line, the high-tide wrack line, and especially on barnacle-covered rocks and sand, mud, and weed-littered flats.

The turnstones typically appeared and started foraging as soon as the falling tide began to expose the tidal flats and continued foraging until the rising tide covered the feeding ground. Barnacle-covered rocks ranging from small fragments to large glacial erratics were dominant features of the low tide topography. Barnacles (*Balanus balanoides*), a major turnstone food, were abundant on these rocks, as was rockweed (*Fucus vesiculosus*). Several times during the study, high seas and storm-driven waves deposited large quantities of algae (*Ulva lactuca* and *Chondrus crispus*), eel grass (*Zostera marina*), and an associated fauna of marine invertebrates over the exposed tidal flats, especially at the high tide line. These accumulations of invertebrate-infested algae and eel grass persisted as long as a week and were frequented by foraging turnstones.

Through the fall migration, mid-July to early October, data were gathered on 286 turnstones (164 adults, 122 juveniles) during nearly daily observation periods from 5 August to 25 September 1974. The data gathering techniques were refined from methods used in preliminary studies of 139 turnstones during the same period in 1973. (The 1973 data on turnstone postures are included here, but the 1973 foraging data lack details on various components of foraging discussed here, so they are omitted.)

Daily observation periods ranged from 30 to 180 min. Individual birds were watched for periods of 30 to 1,500 sec with a 20 × spotting scope and timed to the nearest second with a stop watch. As soon as the identity of an individual bird became uncertain the observation was ended and a new subject selected arbitrarily. Each bird's age and plumage were noted, the habitat characterized, the number and ages of turnstones around the subject noted, and the estimated size of the area occupied by a group of turnstones (1–25 m²) recorded. Throughout each observation the bird's posture and postural changes were recorded as were the occurrence and outcome of all interactions with other birds.

In Massachusetts, fall migrant adult and juvenile Ruddy Turnstones are readily distinguished by plumage characteristics. All adults seen during the fall migration were in predominantly alternate plumage, and most had obvious feather wear. (Of 37 adult turnstones trapped during this period, several birds had arrested molt with a few basic contour feathers in the body plumage, but none showed active molt.) Juveniles, which did not begin arriving until mid-August, were in the more subdued and uniformly colored fresh juvenal plumage.

Up to 20 different birds were watched daily. Many of the same individuals were doubtless seen on subsequent days, but because of the impossibility of identifying individuals positively from day to day, it was necessary to evaluate each timed observation of a bird as a separate case. About 30 turnstones were color-banded with unique combinations to facilitate individual identification, but only one of these birds was ever seen more than a day after banding.

TURNSTONE FORAGING TECHNIQUES

Turnstones foraged most commonly on barnacle-covered rocks, frequently in patches of abutting barnacles. Typically a foraging turnstone selects a barnacle and with the mandibles held close together rapidly delivers one or two sharp blows to the upper (e.g. tergal and scutal) plates of the barnacle, which usually suffice to open the barnacle. The flesh is then eaten by a sequence of pecks into the open barnacle with occasional movements to remove pieces of broken plates. Extensive pecking and maneuvering around the barnacle with the bird's head tilted through various angles is common, presumably to clean out as much of the barnacle flesh as possible. Often a series of barnacles consumed by a turnstone are close or adjacent to each other, and a bird may remain within a small space (approximately 50 cm × 50 cm) on one rock for 20 min or more. On occasion a turnstone will peck among the plates of a dead barnacle or displace another feeding turnstone from a barnacle and feed in the barnacle opened by the displaced bird.

Birds also foraged on tidal flats varying from clear open sand and mud flats with scattered patches of growing eel grass to shores thickly covered with tide-cast eel grass and algae. Various crustaceans (shrimp, crabs, amphipods) and polychaete worms were locally abundant on the sand flats and in the vegetation.

On sand and weed-littered flats, turnstones locate prey by directed foraging move-

ments including flicking up pieces of weed with the bill, using the bill to peck or dig in the sand, overturning piles of weed by lunging forward and pushing with the bill and forehead, and flipping stones with an upward movement of the bill. Several manipulations of the substrate and prey may precede a prey capture.

Sand and weed-littered flats represent more heterogeneous foraging situations than barnacle-covered rocks. Qualitative examination of the substrate and quantitative observations of foraging birds show the inconspicuous invertebrate population to be patchily distributed through the sand, mud, and weed litter. Procuring food in such a situation is relatively more complex than feeding on barnacles, and involves active searching for a variety of acceptable prey items, pursuing, and capturing mobile crustaceans and worms.

Two types of foraging activities were classified and recorded during observations of individual birds. (1) Each foraging movement involving contact of the bird's bill with the substrate or manipulation of the substrate in search of food was a directed foraging movement (F). These movements included using the bill to flick over pieces of weed, overturn rocks, and peck in the sand as well as unsuccessful attempts to capture single prey items. Unfortunately, frequent difficulties in distinguishing clearly between searching activities and unsuccessful attempts to capture prey, especially on weed-littered flats, necessitated classifying these two activities together as directed foraging movements. (2) A single foraging movement resulting in the ingestion of a prey item was a prey capture (P). In the field prey captures were readily identified, as many prey items such as barnacles, crustaceans, and worms were visible to the observer when a bird (usually) lifted its head and paused while making a visible swallowing movement.

The following manipulations were performed on the data to obtain measurements of foraging rates and efficiency for each bird observed (t = time in sec): (1) foraging rate = $(P + F)/t$; (2) success rate = P/t ; (3) frequency of success = $P/(P + F)$. Results were analyzed by the Mann-Whitney U -test and Chi-square one sample test (Siegel 1956).

Birds in the two foraging situations, barnacle-covered rocks and sand and weed-littered flats, were considered separately as foraging rates in the two situations showed highly significant, age-independent differences (Table 1, $P < 0.001$, Mann-Whitney U -test). Adults and juveniles were compared in each foraging situation. The results, presented in Table 1, show statistically significant differences in the foraging and success rates of adults and juveniles; the time-independent frequencies of success are nearly equivalent.

DISCUSSION

The results indicate that foraging rates but not success rates vary significantly in different habitats and that regardless of habitat, juvenile Ruddy Turnstones are not as adept as adults at procuring food. Although approximately equivalent proportions of foraging movements in both age classes result in ingestion of prey items, the two age groups differ in the rates at which they forage and capture prey. This suggests that experience in searching for and mechanically extracting and handling prey may be a primary factor accounting for the observed differences in foraging and success rates.

It has been suggested that foraging ability in birds improves with age and experience (Ashmole 1963) and further, that foraging inefficiency is a major factor con-

TABLE 1
FORAGING RATES, SUCCESS RATES, FREQUENCIES OF SUCCESS OF TURNSTONES ON TWO SUBSTRATES

| | | Barnacle-covered rocks | | |
|--|-----------|------------------------------|---------------------|----------------------|
| | | Adults, $N = 108$ | Juveniles, $N = 78$ | All birds, $N = 186$ |
| Foraging rate, $\frac{P + \bar{F}}{t}$ | range | 0.066–0.545/sec | 0.015–0.364/sec | 0.015–0.545/sec |
| | \bar{x} | 0.222/sec | 0.188/sec | 0.208/sec |
| | SD | 0.070/sec | 0.069/sec | 0.072/sec |
| $z^1 = 3.39, P < 0.001$ | | | | |
| Success rate, $\frac{P}{t}$ | range | 0.044–0.478/sec | 0.000–0.364/sec | 0.000–0.478/sec |
| | \bar{x} | 0.185/sec | 0.156/sec | 0.173/sec |
| | SD | 0.069/sec | 0.069/sec | 0.070/sec |
| $z = 3.12, P < 0.01$ | | | | |
| Frequency of success, $\frac{P}{P + \bar{F}}$ | range | 0.273–1.000 | 0.000–1.000 | 0.000–1.000 |
| | \bar{x} | 0.814 | 0.812 | 0.813 |
| | SD | 0.137 | 0.196 | 0.164 |
| $\chi^2 = 0.10, NS$ | | | | |
| | | Sand and weed-littered flats | | |
| | | Adults, $N = 36$ | Juveniles, $N = 31$ | All birds, $N = 67$ |
| Foraging rate, $\frac{P + \bar{F}}{t}$ | range | 0.049–1.652/sec | 0.043–0.667/sec | 0.043–1.652/sec |
| | \bar{x} | 0.375/sec | 0.246/sec | 0.315/sec |
| | SD | 0.281/sec | 0.140/sec | 0.235/sec |
| $z = 2.34, P < 0.05$ | | | | |
| Success rate, $\frac{P}{t}$ | range | 0.000–1.000/sec | 0.000–0.383/sec | 0.000–1.000/sec |
| | \bar{x} | 0.258/sec | 0.158/sec | 0.211/sec |
| | SD | 0.203/sec | 0.106/sec | 0.172/sec |
| $z = 2.07, P < 0.05$ | | | | |
| Frequency of success, $\frac{P}{P + \bar{F}}$ | range | 0.000–1.000 | 0.000–1.000 | 0.000–1.000 |
| | \bar{x} | 0.645 | 0.603 | 0.626 |
| | SD | 0.253 | 0.230 | 0.242 |
| $\chi^2 = 0.93, NS$ | | | | |

¹ z = standard normal variate calculated from Mann-Whitney U -test.

² Foraging rates of all birds on barnacles vs. all birds on tidal flats, $z = 3.98, P < 0.001$.

tributing to high mortality in young birds, but until recently there has been little quantified evidence to confirm or refute this hypothesis. Four recent studies have demonstrated age-related differences in foraging efficiency and success in Brown Pelicans, *Pelecanus occidentalis* (Orians 1969), Little Blue Herons, *Florida caerulea* (Recher and Recher 1969), Sandwich Terns, *Sterna sandvicensis* (Dunn 1972), and Royal Terns, *Sterna maxima* (Buckley and Buckley 1974).

In these four species, juveniles are less efficient foragers than conspecific adults in comparable situations. The data available indicate that the observed disparities between adults and juveniles may be attributed mainly to differences in foraging rates (rates of searching, diving, etc.) and the degree of refinement of foraging and prey handling techniques (height of dives, frequency of dropping prey, etc.) and suggest that experience with prey may attenuate these differences.

One consequence of less efficient foraging may be that juveniles obtain less food than conspecific adults in comparable situations. In some species such as the Royal Tern (Ashmole and Tovar 1968), extended parental care may partially compensate for any food deficit. There may be instances of independent juveniles compensating for differences in the quantity of prey obtained by foraging for longer periods of time than adults as reported in the Royal Tern (Buckley and Buckley 1974), but this does not seem to be the case in Sandwich Terns or turnstones. Dunn (1972) reported that

although further observations are needed, he detected no differences in duration of foraging periods of adult and juvenile Sandwich Terns. Similarly, foraging time available to turnstones in this study was limited by the tides, and both adults and juveniles foraged continuously during the available foraging time.

Data on another intertidal feeder, the European Oystercatcher (*Haematopus ostralegus*) wintering in northern Scotland (Heppleston 1971), provide evidence that under extreme environmental conditions juveniles feeding at slightly lower rates than adults are unable to compensate adequately for any food deficit incurred. In 1965–66 first winter birds accounted for 77% of winter mortality ($N = 29$), apparently from starvation.

If inexperience is the main source of the observed foraging inefficiency of juveniles, then it should follow that with time and maturity juveniles would develop greater proficiency at locating and handling prey, and disparities in foraging efficiencies of adults and juveniles would diminish. Alternatively, the observed differences in foraging efficiencies between adults and juveniles may represent two classes of birds: inefficient juveniles that do not survive to adulthood and adults. Dunn (1972) mentions this possibility in his discussion of Sandwich Terns but then points out that newly fledged terns are notably poor fishers and dependent on parental feeding until migration away from the breeding grounds. Similarly, each year the first juvenile turnstones to appear were decidedly hesitant and somewhat inept in their foraging efforts, but this marked hesitancy disappeared within a few days. Probably the most inefficient juveniles do not reach adulthood, but those that survive their first few months to adulthood improve in their foraging efficiency as they mature.

POSTURES AND AGGRESSIVE INTERACTIONS

Two postures were commonly observed among foraging turnstones. In the tail-level posture (Fig. 1A) the head is upright, the wings are against the body, the tail is held in line with the body axis, and the contour feathers lie smooth and flat. In the tail-depressed posture (Fig. 1B) the tail of the foraging bird is depressed below the body axis with the white of the upper rectrices visible above the dark feather tips. The degree to which the tail is depressed varies among individuals and in different situations. The tail-depressed posture is frequently associated with chasing and aggression. It is sometimes accompanied by lowering of the head and raising of the scapulars, which gives the bird a hunched appearance. In some instances the wings are slightly drooped and held away from the body.

Aggressive interactions are most often seen among turnstones in typical foraging groups ranging from 2–3 up to 20 birds. Such interactions usually last only a few seconds and occur when the foraging paths of two birds intersect. The encounter may involve posturing or chasing. Physical contact involving pecking and grabbing of the opponent with the feet occasionally occurs. Aggressive interactions end when one bird moves away from the encounter site. In all observed interactions involving adults and juveniles the adult was always dominant, and the juvenile moved away from the encounter site. Occasionally a turnstone will approach and displace a feeding turnstone and then eat the prey item the displaced turnstone left, but in most cases, aggressive interactions do not appear to be centered around particular food items. Violations of individual distance or feeding territories may explain some aggressive interactions.

The numbers and ages of birds foraging together were recorded to provide data on

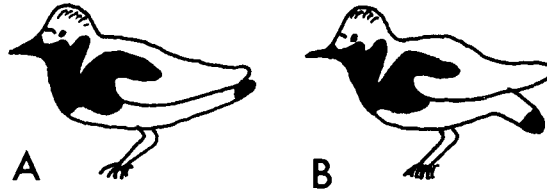


Fig. 1. Postures of turnstones: A, Tail-level posture; B, Tail-depressed posture.

the social context in which aggressive interactions occur. All interactions were identified by type according to ages of the participants and outcomes of interactions: adult over adult, adult over juvenile, juvenile over adult, juvenile over juvenile.

From 14 August to 12 September when both adults and juveniles were present, expected frequencies of each possible type of aggressive interaction were predicted on the basis of the number of adults and juveniles present in observed groups of turnstones. The model used by Ridpath (1972) to predict frequencies of age-related interactions was applied to the data in this study.

For a mixed adult and juvenile flock of any specified composition

$$p = \text{number of adults}/(\text{number of adults} + \text{juveniles}),$$

$$q = \text{number of juveniles}/(\text{number of adults} + \text{juveniles}),$$

and

$$p + q = 1.$$

Assuming random occurrence of all types of aggressive interactions, $p^2 + 2pq + q^2 = 1$ predicts the expected frequencies of aggressive interactions where p^2 represents all adult over adult interactions, q^2 represents all juvenile over juvenile interactions, and $2pq$ represents all adult over juvenile and juvenile over adult interactions. It is important to note that no juvenile over adult interaction was ever observed.

During the timed observations of foraging birds, detailed notes on posture and aggressive interactions were obtained on 286 turnstones. Among these birds, those in

TABLE 2
POSTURES OF TURNSTONES AND DOMINANCE IN AGGRESSIVE INTERACTIONS

| Posture | Age | No. of birds observed in posture | No. of birds dominant in aggressive interaction |
|-----------------------------|----------|----------------------------------|---|
| 1973 ¹ | | | |
| Tail-level ³ | Adult | 32 | 1 |
| | Juvenile | 21 | 2 |
| Tail-depressed ⁴ | Adult | 45 | 23 |
| | Juvenile | 41 | 15 |
| 1974 ² | | | |
| Tail-level ⁵ | Adult | 74 | 6 |
| | Juvenile | 54 | 3 |
| Tail-depressed ⁶ | Adult | 90 | 25 |
| | Juvenile | 68 | 15 |

¹ Tail-level vs. tail-depressed, $\chi^2 = 16.50$, $P < 0.001$.

² Tail-level vs. tail-depressed, $\chi^2 = 13.80$, $P < 0.001$.

³ Adult vs. juvenile, $\chi^2 = 0.91$, NS.

⁴ Adult vs. juvenile, $\chi^2 = 1.03$, NS.

⁵ Adult vs. juvenile, $\chi^2 = 0.29$, NS.

⁶ Adult vs. juvenile, $\chi^2 = 0.51$, NS.

TABLE 3
SUMMARY OF FLOCK COMPOSITION AND FREQUENCY OF TYPES OF AGGRESSIVE INTERACTIONS

| Flock composition | | | Aggressive interactions | | | |
|-------------------|------------------|--------------|-------------------------|---------------------|---------------------|------------------------|
| No. of adults | No. of juveniles | No. of cases | Adult over adult | Adult over juvenile | Juvenile over adult | Juvenile over juvenile |
| 17 | 1 | 1 | 1 | — | — | — |
| 6 | 2 | 1 | 5 | 4 | — | 1 |
| 5 | 1 | 1 | 1 | 1 | — | — |
| 4 | 1 | 2 | 6 | 3 | — | — |
| 4 | 2 | 3 | 3 | 11 | — | 2 |
| 4 | 3 | 1 | 2 | — | — | — |
| 3 | 1 | 1 | 2 | 2 | — | — |
| 3 | 2 | 1 | — | 2 | — | — |
| 2 | 1 | 2 | 4 | 6 | — | — |
| 2 | 2 | 3 | — | 6 | — | 1 |
| 2 | 3 | 1 | — | 1 | — | 1 |
| 2 | 4 | 2 | — | 5 | — | 2 |
| 1 | 1 | 1 | — | 1 | — | — |
| 1 | 2 | 2 | — | 5 | — | 1 |
| 1 | 4 | 1 | — | 4 | — | — |
| 1 | 5 | 1 | — | 2 | — | — |

the tail-depressed posture were dominant in aggressive interactions much more often than those in the tail-level posture (Table 2, $\chi^2 = 13.80$, $p < 0.001$). Likewise, during the preliminary observations of 139 turnstones in 1973, birds in the tail-depressed posture were dominant in aggressive interactions much more often than birds in the tail-level posture (Table 2, $\chi^2 = 16.50$, $p < 0.001$). No age-related differences in the frequency with which adults and juveniles in the tail-level or tail-depressed postures were dominant in aggressive interactions were noted in either year (Table 2).

Aggressive interactions occurred in 24 of 37 mixed adult and juvenile flocks observed. For each of these flocks of known-age composition, the observed frequencies of each type of aggressive interaction (Table 3) were compared to the calculated expected frequencies. For all 24 flocks and each possible type of interaction the directions of deviations from expected frequencies were tallied (Table 4) and evaluated by the sign test (Siegel 1956). During the period when adults and juveniles were present together, adult over adult interactions were seen less frequently than expected ($P = 0.002$) as were juvenile over juvenile interactions ($P = 0.022$). Interactions involving adults and juveniles occurred more frequently than expected ($P = 0.006$) and were always of the adult over juvenile type.

TABLE 4
COMPARISON OF OBSERVED AND EXPECTED FREQUENCIES OF DOMINANCE IN AGGRESSIVE INTERACTIONS IN 24 MIXED-AGE FLOCKS OF TURNSTONES

| | p^2 Adult over adult | $2pq$ | | q^2 Juvenile over juvenile |
|-----------------------------|------------------------------|------------------------|------------------------|------------------------------------|
| | | Adult over juvenile | Juvenile over adult | |
| Obs. > Exp. | 4 | 19 | — | 6 |
| Obs. = Exp. | 0 | 0 | — | 0 |
| Obs. < Exp. | 20 | 5 | — | 18 |
| P (sign test, two-tailed) | 0.002 | 0.006 | — | 0.022 |

DISCUSSION

In mixed flocks of adult and juvenile turnstones the observed frequencies of possible types of aggressive interactions are nonrandom. The higher than expected frequency of adult over juvenile interactions suggests that dominance in aggressive interactions is age-related. Interactions involving adults and juveniles always ended with the juvenile moving away from the encounter site. Ridpath (1972) observed similar behavior in the Tasmanian Native Hen (*Tribonyx morterii*), specifically that conflicts between adults and young are more frequent than would be expected if conflicts are independent of age, and they are always initiated and won by adults.

The lower than expected frequency of juvenile over juvenile and adult over adult aggressive interactions raises the possibility that either juvenile turnstones are somehow inept at avoiding adults or that adults are selectively aggressive towards juveniles. As adults stay with their young on the breeding ground during the pre-fledging period in late July (Nettleship 1973), apparent ineptness of juveniles at avoiding adults may be a vestige of their recent period of presumably aggression-free association with their parents. In encounters with adults in foraging south of their nesting grounds, juveniles may take time to learn that the context in which they interact with adults has changed.

Young Adelie Penguins (*Pygoscelis adeliae*) are reported to respond inappropriately to messages conveyed by the displays of other conspecifics, especially adults (Ainley 1975). Similarly, juvenile Ruddy Turnstones may be responding inappropriately to messages conveyed behaviorally by adults. For instance, an adult turnstone may communicate by its posture, especially the tail-depressed posture, that it is likely to respond aggressively to any bird approaching within a certain distance. A juvenile turnstone may misinterpret or respond ambivalently to this message and thus approach an adult close enough to become the subject of aggression. If juveniles commonly misinterpret or respond ambivalently to such messages, this could account for the unexpectedly high frequency of adult over juvenile aggressive interactions.

Presumably juveniles learn to avoid aggression by adults and behave less ambivalently in the presence of adults, but the transiency of fall migrants coupled with the lack of observations of marked individuals made assessment of the persistence of nonrandom aggression in mixed-age flocks of turnstones unfeasible in this study. For similar reasons, the cost to a juvenile of involvement in frequent aggressive interactions could not be measured in terms of lost foraging time.

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