EXPERIMENTAL REMOVAL AND REPLACEMENT OF TERRITORIAL MALE YELLOW-BREASTED CHATS

CHARLES F. THOMPSON

ABSTRACT.—Systematic mist netting of male and female Yellow-breasted Chats on study tracts in southern Indiana and northeastern Georgia revealed that unbanded birds were captured regularly after the end of spring migration. Resettlement of males on experimentally vacated territories demonstrated that the new arrivals were potential settlers that normally were excluded from settling by established males, and these potential settlers were probably not members of a nonbreeding surplus population. Because of the importance to general theory of the existence of surplus populations, it was emphasized that the existence of potential settlers was necessary but not sufficient evidence that a nonbreeding surplus population existed. The removal experiments demonstrated that the number of breeding males was normally limited in some habitats by the presence or resistance of established males.—*Department of Zoology, Indiana University, Bloomington, Indiana 47401, and Department of Zoology, University of Georgia, Athens, Georgia 30602. Present address: Department of Biology, State University College, Geneseo, New York 14454*. Accepted 14 July 1975.

THE last decade has seen renewed interest in the idea that territorial behavior may play an important role in limiting the size of breeding bird populations (e.g. Fretwell 1969, Brown 1969, Watson and Moss 1970, Klomp 1972, Maynard Smith 1974). Brown (1969), Krebs (1971), and Klomp (1972) made the important distinction between the role that territorial behavior may play in limiting the size of an entire species population and its role in limiting population size on a local scale. Klomp (1972) pointed out that the breeding population as a whole is limited by territorial behavior only if all available habitat is saturated and excluded birds are forced to join a nonterritorial, or landless, population; on the other hand, if birds are excluded from the most suitable habitats, but not from the less suitable habitats, or if no birds are excluded from any habitat, the entire species population is not limited by territorial behavior and no nonterritorial surplus occurs. Therefore the demonstration in any species of the existence of unsettled individuals capable of settling and breeding if given the opportunity takes on considerable importance, for it suggests that landless, surplus birds may be present, which within the framework of current models implies that the breeding population is limited by territorial behavior (Brown 1969, Watson and Moss 1970, Klomp 1972).

It was of great interest, then, when systematic mist netting of Yellow-breasted Chats (*Icteria virens*) on a study tract in southern Indiana revealed that unbanded newcomer males and females were caught throughout the breeding season (Thompson and Nolan 1973); perhaps these birds were potential settlers and members of a surplus population. Further observation established the following (Thompson and Nolan 1973): Only about 30% of the males and females first captured after spring migration settled on the area; the rest were transients. Those males that did settle after spring migration established territories in space vacated by males that had failed to obtain or had lost a mate; and most of the new females replaced other females that had disappeared after their nests failed. Some vacancies created by disappearances were never filled. The reproductive output of the population was low, and it seemed probable that the study tract was unfavorable chat habitat.

In view of the evidence outlined above, the occurrence and status of apparently

unsettled adult chats was investigated further by determining (1) whether such individuals were present after spring migration in other localities and (2) whether, if so, many or most were potential settlers, i.e. birds able and willing to settle. The former point was investigated by systematically mist-netting a chat population in northeastern Georgia (approximately 800 km southeast of the Bloomington study tract) and the latter by experimentally removing territorial males from six localities in southern Indiana. This paper reports the results of these further studies.

METHODS

Chats were systematically mist-netted from 1967 through 1970 on the Bloomington study tract in southern Indiana and in 1973 at the Athens study tract in the University of Georgia's Botanical Garden in northeastern Georgia. General procedures and placement of nets were similar in both places, except that at Athens only 12-m nets (type ATX of the Northeastern Bird-Banding Association) rather than a combination of 6- and 12-m nets were used; this increased the surface area of netting to which the Athens population was exposed during each net hour by an estimated 13% over Bloomington. For further details of mist-netting procedures see Thompson and Nolan (1973). Bloomington's chat population was exposed during the 4 years to 8084 net hours between 24 April and 2 July; the Athens population was exposed to 1611 net hours during the same period in 1973.

Seven removal experiments of territorial males were performed on six study tracts (fields A through F) in southern Indiana from 1969 to 1971. The number of territorial males present both before and after the removal experiments was estimated by counting singing males and watching their movements during two or more censuses. Because most of the experimental chat populations were not followed closely, it was difficult to be certain that the censuses were completely accurate. Therefore all estimates of preremoval numbers are maxima and all postremoval numbers are minima; this results in the most conservative estimate of the number of males that recolonized the experimentally vacated areas. Females were not systematically removed. Males, and occasionally females, were shot when they were attracted by the playing of tape-recorded songs of the male on their territories.

Two types of removal experiments were performed: (1) In single removals, males were shot on only 1 day and the males present 1 to 2 weeks later were counted. (2) In multiple removals, males were shot on 2 or more days, resulting in the removal of both original residents and some replacements; after 1 to 2 weeks the areas were again censused.

STUDY TRACTS

Mist-netting sites.—The Bloomington study tract was a series of upland old fields 18 ha in area that had been last cultivated 15 to 20 years before the study began. The exact location and vegetation are described by Thompson and Nolan (1973).

The Athens study tract was 6.4 km south and 0.8 km west of the Clarke County, Georgia courthouse. Approximately 5.8 ha was floodplain of the middle Oconee River and 5.4 ha the northern wall of the river's valley. The floodplain and valley wall were last cultivated about 6 and 23 years earlier, respectively. Surrounded completely by forest, the tract was an island of old-field habitat broken only by a powerline right-of-way that crossed the eastern edge. Dense, diverse herbaceous vegetation 1–2 m high dominated the floodplain, throughout which were scattered seedlings of privet (*Ligustrum* sp.) as well as loblolly pine (*Pinus taeda*), box elder (*Acer negundo*), and other tree seedlings. The northern edge of the floodplain had dense stands of blackberry (*Rubus* sp.) and old fence-rows overgrown by Japanese honeysuckle (*Lonicera japonica*), blackberries, saplings, and shrubs. The terraced valley wall was a mosaic of planted loblolly pines and clumps of blackberries, honeysuckle, shrubs, and small trees interspersed with eroded areas. Chats used the entire tract, except for the center of the floodplain.

Chats typically are associated with habitats of dense low vegetation, and the most striking difference between the Bloomington and Athens tracts was that the lower stratum (less than 2 m high) of vegetation was generally denser at Athens.

Experimental fields.—Fields A and B were 9.7 km east and 3.6 km south of the Monroe County, Indiana courthouse. Fields C, D, E, and F were in the Crane Naval Ammunition Depot, Martin County, Indiana, approximately 27 km west and 39 km south of the Monroe County courthouse. All experimental fields were patches or strips of old-field habitat of less than 10 ha surrounded by forest or grassland uninhabited by chats. Other patches of suitable chat habitat were nearby. The experimental fields were

chosen to include most of the range of old-field habitats occupied by chats in southern Indiana. The principal vegetation of each area was as follows: Field A, planted pines (*Pinus* sp.) scattered among fairly open deciduous growth. Field B, central area densely planted in pines 3–4 m high; dense deciduous growth among and bordering the pines. Field C, open old-field vegetation and a long border of deciduous shrubs and saplings about 10 m wide between forest and grassland. Field D, grassy field with dense deciduous growth in one corner. Field E, dense deciduous shrubs and saplings with scattered red cedars (*Juniperus virginiana*). Field F, dense deciduous shrubs and saplings with two dense stands of 4 m high planted pines.

RESULTS

Arrival and settlement.—There were differences, as expected, between the Bloomington and Athens populations with respect to the dates of arrival and first breeding. The first males arrived in Athens between 23–26 April 1973, whereas the earliest arrival in Bloomington was 30 April. The earliest clutch was begun in the second week of May in both places, although at Bloomington breeding usually did not begin until the third week of May (Thompson and Nolan 1973). A more detailed comparison of the timing of the breeding seasons is not possible because only 1 year's data are available from Athens.

The pattern of the seasonal distribution of captures of unbanded male and female chats was similar for both Bloomington and Athens (Fig. 1). In both places the peaks of spring migration for both sexes, i.e. the arrival of residents and the passage of spring transients, occurred during the first half of May. At both locations the arrival of males and females overlapped, although the peak of male captures was slightly earlier than that of females. Most important, in both places the conclusion of spring migration was followed in late May and early June by a period during which unbanded males and females were also caught. In Bloomington this was reflected as an increase in capture rates during 5–11 June that was presumably equivalent to the increase at Athens between 29 May–11 June.

In Bloomington most of the males that successfully established territories did so during the spring migratory period (Thompson and Nolan 1973). Although individual birds were not followed as closely at Athens, two observations support the conclusion that there, too, most of the resident males settled during spring migration: (1) Of 6 banded territorial males known to be present after 1 June, 5 were first captured before 15 May, and (2) only 1 male first captured after 14 May was subsequently recaptured or seen. This male settled in a territory that another male had abandoned earlier in the season.

The timing of the settlement of females both during and after spring migration also appears to have been similar in both places. Based on recaptures, some females that arrived in late May and early June at Athens settled and bred, just as they did at Bloomington. At Bloomington (Thompson and Nolan 1973: 153–155), 20 of 21 females and at Athens, 6 of 7 females first captured after the conclusion of spring migration had a brood patch. Therefore in both places most of these females probably had nested earlier in the season.

Capture rates for both sexes were higher at Athens (males = 1.4, females = 1.4 per 100 net hours) than at Bloomington (males = 0.9, females = 0.9 per 100 net hours) during the same 10-week period. This difference in capture rates was not caused by the 13% increase in the surface area of mist nets at Athens (see Methods), for this would account for only about 20% (0.1 bird per 100 net hours) of the difference in capture rates; it probably was caused by a combination of greater

TABLE 1

REMOVAL AND REPOPULATION OF MALE YELLOW-BREASTED CHATS ON SIX STUDY AREAS IN SOUTHERN INDIANA

Field	Removal dates	Estimated maximum no. males before removal	Total no. of males removed	Estimated minimum no. of males 1–2 weeks later	Minimum no. of new males[1]
Single removals[2]					
A	5 June 1969	2	2	1	1
C	4 June 1970	8	7	5	4
D	31 May 1970	2	2	1	1
E	8 June 1971	3	4	3	4
TOTALS		15	15	10	10
Multiple removals[2]					
B	10, 12, 25 June 1969	3	5	?[3]	2
E	2, 3, 13 June 1970	7	12	3	8
F	31 May; 8, 14 June 1970	3	8	2	7
TOTALS		13	25	5	17

[1] Calculated by subtracting column 3 from column 4 and adding column 5.
[2] Explained in the text.
[3] Unknown because males had reduced their singing activity.

movement of chats through the Athens tract and slight differences between the tracts in the crude densities (Odum 1971: 166) of territorial males (Athens = 18–25 males, Bloomington = 11–20 males per 40 ha) (MS, Thompson and Nolan 1973).

Removal experiments.—The results of the 7 experiments in which territorial males were shot after the end of the spring migratory period are summarized in Table 1. In the 4 single removal experiments, at least 10 males replaced the 15 males that were shot; this level of replacement was achieved within 2 weeks after removal. In multiple removal experiments, 25 males were shot from tracts that had supported only 13 original males; 1 to 2 weeks later the tracts had at least 5 males, so a minimum of 17 (12 + 5) new males resettled the tracts after the original residents were killed.

The 1971 experiment in field E (Table 1) is particularly interesting because 2 of the 3 original territorial males had been banded earlier in the season. On the morning of 8 June, the 2 banded males as well as 2 unbanded males were shot. As only 3 males (2 banded and 1 unbanded) had been holding territories on the field at the beginning of the removals, the unexpected additional unbanded male apparently moved in and began singing during the shooting. This new male was killed while singing on land that had been within the territory of a male that I had shot only 30 min earlier. Further repopulation was rapid: The next morning three new males were singing on the tract, one of which obtained a mate that later successfully raised a brood. Direct confirmation of breeding by other replacements in other experiments was not obtained, but indirect evidence (e.g. behavior of the male and presence of females) indicated that many did breed.

DISCUSSION AND CONCLUSIONS

Arrival and settlement.—The general timing and pattern of arrival, settlement, and breeding of chats was similar at both Bloomington and Athens, although the Athens population was about 1 week ahead of the Bloomington population.

The results from mist netting at Athens revealed the presence of unbanded male

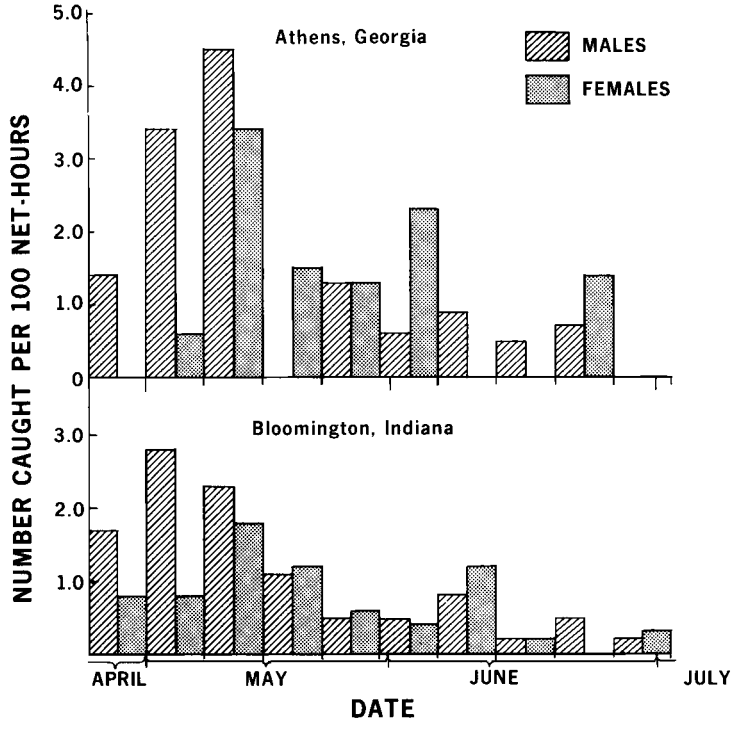

Fig. 1. Number of unbanded male and female Yellow-breasted Chats captured per 100 net hours at Athens, Georgia in 1973 and at Bloomington, Indiana from 1967 through 1970. The lower half is a modification of Fig. 2 in Thompson and Nolan (1973).

and female chats after spring migration, which is consistent with and confirms the findings at Bloomington. Most of these birds did not settle on the study tracts. At Bloomington only about 30% of the adults first captured after spring migration settled; at Athens the less complete data suggest a similar low incidence of late settlement. At Bloomington and apparently at Athens proportionately fewer late-arriving males than females settled to breed. Thus evidence from two separate regions within the chat's breeding range shows that birds not established on the local study tract were present after spring migration and that few of these late arrivals settled. That all of these events may be general features of breeding populations of chats is bolstered further by R. Beck's (1974 in litt.) observations, based on intensive mist netting, that late arrivals also occurred but seldom settled at Williamsburg, Virginia.

Potential settlers.—The demonstration of the existence of landless birds and their occasional successful settlement does not tell us whether most are potential settlers. The results of the removal experiments in which territorial males were killed and rapidly replaced do support the hypothesis that many late arrivals were indeed potential settlers able and willing to settle vacant habitats. Breeding by at least one and probably more settlers suggests that many were fully able to attract and successfully inseminate a mate. At Bloomington some of the males that settled in naturally created vacancies did not breed (Thompson and Nolan 1973: 154); although some of these territorial, nonbreeding males may have been unable to attract a mate, it is also possible, and I think more likely, that late in the season there was a dearth of unsettled and receptive females (see Fig. 1). Nonetheless, with the available data it is

not possible to conclude whether all potential male settlers could breed if given the opportunity, but many certainly did. Females readily settled in naturally created vacancies after spring migration, suggesting that most late arrivals also were potential settlers, but this conclusion was not tested experimentally.

What precludes newly arriving males from settling? The removal experiments support the earlier suggestion (Thompson and Nolan 1973: 166) that either the behavior or merely the physical presence of the resident males is important in blocking settlement of new males. Although the relative importance for the chat of these two factors cannot be determined from present information, tranquilization experiments on Black-headed Gulls (*Larus ridibundus*) by Patterson (1965) and on Red-winged Blackbirds (*Agelaius phoeniceus*) by Peek (1972) revealed that behavioral attributes rather than mere presence were necessary to maintain a territory and to exclude intruders; and Krebs (1971) suggested that song advertisement by territorial male Great Tits (*Parus major*) was probably sufficient to prevent nonresidents from attempting to settle.

Origin of potential settlers.—The demonstration of the existence of potential settlers in breeding populations of chats raises the important question of the origin of these birds. Thompson and Nolan (1973: 166) suggested three possible, but not mutually exclusive, origins for potential settlers: (1) a subpopulation of nonbreeding, landless, or surplus individuals; (2) nearby territory holders exploring new lands; and (3) former territory holders that had abandoned territories they had held earlier in the season. It was concluded from observational evidence (Thompson and Nolan 1973: 166) that the latter two possibilities were the more likely and that a surplus existed was unlikely. While the removal experiments were not designed to distinguish among these possibilities and only further study will reveal conclusively the origin of potential settlers, it is clear that the demonstration of the existence of potential settlers is necessary but not sufficient evidence to show that a nonbreeding surplus, or "floating," population exists. Other possibilities exist that must be investigated and eliminated before we can conclude with any certainty that a surplus is present.

Although many authors have recognized this and have clearly distinguished between evidence for potential settlers and for nonterritorial, nonbreeding surplus individuals (Nolan 1963, Watson and Moss 1970, Krebs 1971, von Haartman 1971, Klomp 1972), others have not. For example, Stewart and Aldrich (1951) and Hensley and Cope (1951) interpreted the results of their removal experiments as demonstrating the existence of an unsettled surplus, an interpretation that has been accepted and cited by others (e.g. Wynne-Edwards 1962: 148; Harris 1970; Collier et al. 1973: 190; Ricklefs 1973a: 220). In fact, these experiments revealed only the presence of potential settlers of unknown origin. The importance of this distinction should not be minimized, because in current models of population regulation the demonstration of surplus birds capable of settling and breeding implies that individuals are being excluded from breeding sites, presumably by territorial behavior, and are thereby limiting the size of the total breeding population of the species (Brown 1969, Watson and Moss 1970, Klomp 1972). While it is possible to criticize this inference (surplus birds might occur if patches of suitable habitat were sufficiently scattered so that the dispersal powers of excluded birds were not adequate to allow them to find all the patches), the existence of surplus birds of whatever origin is clearly important to any consideration of avian population dynamics (Ricklefs 1973b: 378).

Population regulation.—The removal experiments after spring migration dem-

onstrated the existence of potential settlers capable of settling and breeding, but normally prevented from doing so by the presence or resistance of established males. Therefore irrespective of the origin of the potential settlers, established males clearly limited the local population density by excluding some birds. Whether this is true for the entire species population is unknown (see Thompson and Nolan 1973: 166–167).

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LITERATURE CITED

BROWN, J. L. 1969. Territorial behavior and population regulation in birds. A review and re-evaluation. Wilson Bull. 81: 293–329.

COLLIER, B. D., G. W. COX, A. W. JOHNSON, & P. C. MILLER. 1973. Dynamic ecology. Englewood Cliffs, New Jersey, Prentice-Hall.

FRETWELL, S. D. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Inst. Stat., Mimeogr. Ser. 642. North Carolina State Univ., Raleigh, North Carolina.

HARRIS, M. P. 1970. Territory limiting the size of the breeding population of the Oystercatcher (*Haematopus ostralegus*)—a removal experiment. J. Anim. Ecol. 39: 707–713.

HENSLEY, M. M., & J. B. COPE. 1951. Further data on removal and repopulation of the breeding birds in a spruce-fir forest community. Auk 68: 483–493.

KLOMP, H. 1972. Regulation of the size of bird populations by means of territorial behaviour. Netherlands J. Zool. 22: 456–488.

KREBS, J. R. 1971. Territory and breeding density in the Great Tit, *Parus major* L. Ecology 52: 2–22.

MAYNARD SMITH, J. 1974. Models in ecology. Cambridge, England, Cambridge Univ. Press.

NOLAN, V. JR. 1963. An analysis of the sexual nexus in the Prairie Warbler. Proc. 13th Intern. Ornithol. Congr.: 329–337.

ODUM, E. P. 1971. Fundamentals of ecology, third ed. Philadelphia, W. B. Saunders.

PATTERSON, I. J. 1965. Timing and spacing of broods in the Black-headed Gull *Larus ridibundus*. Ibis 107: 433–459.

PEEK, F. W. 1972. The effect of tranquilization upon territory maintenance in the male Red-winged Blackbird (*Agelaius phoeniceus*). Anim. Behav. 20: 119–122.

RICKLEFS, R. E. 1973a. Ecology. Newton, Massachusetts, Chiron Press.

———. 1973b. Fecundity, mortality, and avian demography. Pp. 366–435 *in* Breeding biology of birds (D. S. Farner, Ed.). Washington, D.C., Natl. Acad. Sci.

STEWART, R. E., & J. W. ALDRICH. 1951. Removal and repopulation of breeding birds in a spruce-fir forest community. Auk 68: 471–482.

THOMPSON, C. F., & V. NOLAN, JR. 1973. Population biology of the Yellow-breasted Chat (*Icteria virens* L.) in southern Indiana. Ecol. Monogr. 43: 145–171.

VON HAARTMAN, L. 1971. Population dynamics. Pp. 391–459 *in* Avian biology, vol. 1 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.

WATSON, A., & R. MOSS. 1970. Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. Pp. 167–218 *in* Animal populations in relation to their food resources (A. Watson, Ed.). Brit. Ecol. Soc. Symp. 10. Oxford, Blackwell Sci. Publ.

WYNNE-EDWARDS, V. C. 1962. Animal dispersion in relation to social behaviour. Edinburgh, Oliver and Boyd.