

EXPERIMENTAL MODIFICATION OF REPRODUCTIVE PERFORMANCE BY DENSITY IN CAPTIVE STARLINGS

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Regulation of animal populations by density-dependent factors has received much attention from ecologists. Lack (1966) has examined this problem extensively in natural populations of birds, and contends that reproductive rate, as measured by the number of eggs per clutch, has evolved through natural selection to correspond, on the average, with the number giving rise to the greatest number of offspring. Since clutch size varies little with density, population regulation must, therefore, be a function of density-dependent variations in mortality which in some wild birds correlates well with food shortage.

Lowered fecundity with high population density is rarely reported for avian populations (Kluyver 1951, 1963; Lack 1966; Perrins 1965). It is known, however, that external stimuli associated with breeding behavior in birds can result in changes in the birds' physiological state which might affect fecundity. Birds with a history of domestication are generally used in behavioral studies because of their adaptability to confinement. Experimental tests of hypotheses concerning population regulation in wild birds have not been conducted perhaps due to difficulties in getting large numbers to breed readily in captivity. Thus mechanisms operating at the physiological and behavioral levels in wild birds which might result in reproductive changes and lead to population regulation remain unclear.

European Starlings (*Sturnus vulgaris*) have long been used as experimental animals (Bissonette 1933; Burger 1940; Davis 1957, 1963; Mathewson 1961; Schwab and Lott 1969), but few experiments have been concerned with both sexes. Burger (1942) stated that female Starlings isolated during the normal breeding season laid eggs in laboratory cages, but that three or four pairs of Starlings in 1440 m³ cages did not pair. He implied that space was a factor limiting the potential of the female to complete the reproductive cycle in captivity. Miller (1969) reported the successful breeding of a captive pair of Starlings in a 2.4 × 1.8 × 1.8 m cage, but the nestlings

failed to survive more than a few days, apparently because of dietary deficiencies.

This study represents the first attempt to determine how male and female Starlings held captive under natural light and temperature conditions respond to different densities during the regular breeding season. It is also the first study to test experimentally an hypothesis regarding population regulation with respect to birds, i.e., that high population density can modify reproductive performance in a wild species.

MATERIALS AND METHODS

A preliminary experiment was conducted during the 1968 breeding season to determine whether several male and female Starlings in large aviaries would form pairs and go through the normal sequence of reproductive events. This experiment provided a basis on which to establish high and low density captive populations for comparison the following year.

About 70 of the European Starlings from the preliminary study were used in the experiment conducted in 1969. These birds had been trapped in 1967 near Fresno and Santa Rosa, California. In addition, about 350 Starlings were trapped near Santa Rosa in late summer 1968. All Starlings were housed together, from early October until mid-December 1968, in an outdoor aviary. During October, most of the Starlings developed a disease morphologically similar to avian pox. A few of the most heavily infected individuals were removed from this flock. Symptoms abated after approximately three weeks, with a mortality of less than 5%.

Birds from this aviary were removed, sexed by laparotomy (Risser 1971), banded with a numbered aluminum band, and color banded according to sex. Birds from the preliminary experiment were known to be at least 1.5 years old. As late as mid-October, age could be precisely determined by the presence of juvenal plumage, and especially by the few persistent feathers dorsal to the auricular region. When no juvenal feathers were found, age was determined on the basis of skull ossification (Kessel 1951).

In order to establish captive populations comparable in age structure to a wild population, Kessel's (1957) figures for winter flock composition at Ithaca, New York, were used. No such data were available for winter populations in California. The age ratio thus derived and established in each cage was four adult males, one first year male, three adult females, and one first year female. All birds were released in their respective cages by 1 January 1969. Any bird that died during the course of the experiment was replaced with one of the same sex and age. Five cages contained 10 pairs each for a combined total of 100 birds, and

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FIGURE 1. Separate nest boxes used by captive Starlings in high-density Cage 12.

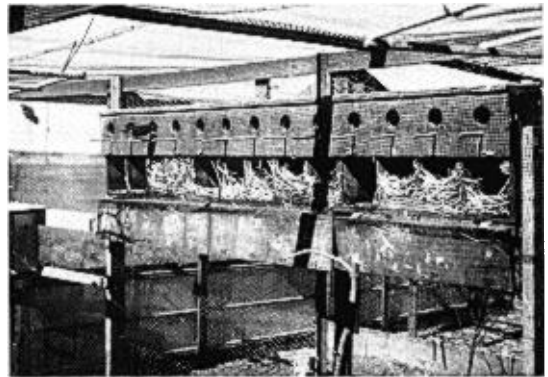


FIGURE 2. Colony-type nest box used by captive Starlings in high-density Cage 3.

two cages contained 50 pairs each for a combined total of 200 birds.

Starlings were caged in two large, outdoor aviaries north of a wooded depression along an old creek bottom in the Zoology Field Area of the University of California, Davis campus. Aviaries consisted of eight adjacent cages, each measuring 6 m long, 3 m wide, and 2.1 m high. Burlap covered the screening between each cage to provide partial visual isolation. There was at least one vacant cage between those that were occupied. Natural vegetation grew from the dirt floor. In each cage there were at least two 1-m hanging horizontal perches.

Each cage was provided with nest sites equal to the number of pairs of birds per cage. Nest boxes in the five 10-pair cages (low-density) and one of the 50-pair cages (high-density cage No. 12, fig. 1) were made of rough 2-cm redwood boards and were of the type and dimensions described by Kessel (1957). Four 13-site colony boxes were erected in the second high-density cage (No. 3). Colony boxes were constructed of 16-mm exterior plywood and coated with redwood stain and varnish. Outside dimensions of the colony boxes were $235 \times 42 \times 20$ cm. Inside dimensions of each compartment approximated those of a separate nest box. Three hinged doors across the bottom provided access to all compartments (fig. 2). A 10-cm horizontal perch was attached perpendicular to the front of each nest site about 4 cm below the hole. The boxes were positioned about 2 m from the floor. Nesting material in the form of straw, burr clover, dried alfalfa hay, and chicken feathers were available at all times.

Commercial turkey pellets with a crude protein content of 27% were always available from hanging self-refilling feeders. Water was also available ad libitum. Fresh vegetables such as tomatoes, squash, apples, parsley, and lettuce were provided occasionally.

Cages were entered daily for nest box inspection, usually between 15:00 and 18:00. Nest-building activity, number of eggs laid, and number of young present were recorded and dead nestlings were removed. From this information mean clutch size per pair, mean total number of clutches laid per pair, and percent hatchability of eggs could be calculated for each density.

In order to compare the temporal pattern of egg production in captive and wild Starlings, nest boxes in the wild used in a study by Planck (1967) were monitored seven times throughout the 1969 breeding season. Additional nest boxes were nailed to power poles and trees along the old creek and nearby cattle

pens south of the aviaries, bringing the number of nest boxes in the field area to 109. These boxes were all within 2 km of the aviaries. Ten boxes attached to the outside of the aviary were checked at least once every 48 hr. First dates of laying were obtained directly from three of these boxes, while laying, hatching, and fledging dates for other boxes in the field area were determined on the basis of the condition of eggs or young in the previous check, and on comparisons with known-aged young. Data from check sheets of workers who monitored nest-box activity during the 1964 through 1967 breeding seasons were combined with the above data to provide a range of laying dates and mean clutch size for Starlings nesting naturally in the vicinity of the aviaries.

To clarify the following presentation of results, a number of terms must be defined. The number of pairs that actually formed at each density was assessed by the number of boxes in which at least one clutch was laid. This method assumes that once a pair nests in a particular box, it will use the same box for subsequent clutches. Although Starlings are usually monogamous, cases of polygamy in nature have been reported (Kessel 1950, 1957).

Familiarity with both pairs in a two-pair cage and one pair in an eight-pair cage in the preliminary experiment supported the conclusion that there was only one breeding pair per nest box. Even if a polygamous male did defend more than one box and mate with more than one female, this measure serves as an index to the females' reproductive performance.

"Clutch size" is used here as defined by Davis (1958): the number of eggs found in a nest. Mean clutch size was calculated only for successful clutches, which are defined as any group of eggs laid in the nest in which at least one egg hatches.

Since even aborted clutches represent reproductive effort by females, abortions were included in calculating the mean number of clutches per breeding pair and total clutches laid in all cages. Generally, aborted clutches were either buried under new nesting material or removed by me some time after the projected hatching date. Eggs were occasionally found on the ground. By checking the previous days' records, it was discovered that the adults expelled most of the eggs from aborted clutches.

Hatchability was recorded as the percent of eggs in the clutch that hatch. No attempt was made to determine if unhatched eggs were fertile.

The interval between the laying of subsequent clutches is defined as the number of days between the death of the last young to the laying of the first egg of

TABLE 1. Mortality in captive Starlings.

	Number of deaths	
	Before 31 May	After 31 May
Low-density cages (20 birds per cage for 5 cages)	9 males (0.18) ^a 2 females (0.04)	2 females (0.04)
High-density cages (100 birds per cage for 2 cages)	None	1 male (0.01) 2 females (0.02)

^a Percent of total males or females for combined cages.

a new clutch. Subsequent nesting cannot be called "renestings" in the usual sense because in this study a successful clutch is one in which at least one egg hatches. A renesting occurs after loss of one of the pair or after the nest is destroyed (Kessel 1957).

RESULTS

VOCALIZATIONS, DISPLAYS, AND AGGRESSIVE BEHAVIOR

Beginning in early January, male Starlings in captivity advertised box ownership and defense with a peculiar crowing, consisting of a raspy chuckle interspersed with whistles. The bill was usually pointed upwards, and the throat feathers extended. Wing tips drooped slightly and quivered. The call appears to be identical to that described by Ellis (1966). Intensity of these displays frequently increased when the cage was entered.

The aerial chase is an integral part of the Starling breeding behavior pattern. This chase consists of two birds, sometimes three, engaged in a rapid, flying pursuit. Hilton (1958) observed that either sex may initiate the flight, which begins from the top of the trees after a series of rapid movements up the branches. That sufficient space in which to conduct the aerial chase is a critical factor for successful reproduction is suggested by the following case. Two pairs of birds, each in a cage 60 × 60 × 90 cm, and provided with a nest box and nesting material (including green leaves), were kept from mid-March to late May under natural light and temperature conditions. The nest box in one cage was unused; the other contained only a few pieces of straw at the end of this time.

The "personal songs," i.e., songs or phrases of other species imitated by Starlings, differed from those reported by Davis (1959), and probably reflect regional differences in species associations. One of the most commonly mimicked calls of captive Starlings in this study was that of the California Quail (*Lophortyx californicus*) which was given with such frequency and clarity by certain individuals as to

suggest its adoption into the normal repertoire. Other species whose calls in part were mimicked included the Acorn Woodpecker (*Melanerpes formicivorus*); Red-shafted Flicker (*Colaptes cafer*); White-crowned Sparrow (*Zonotrichia leucophrys*); Killdeer (*Charadrius vociferus*); Red-tailed Hawk (*Buteo jamaicensis*); and Ring-necked Pheasant (*Phasianus colchicus*).

Whenever fresh green material such as burr clover was placed on cage floors, the birds, particularly males, flocked to it, and, taking a sprig in their bill, paraded around the floor of the cage or flew up to perch on a box. Birds were frequently observed taking greens into boxes.

Although the use of green material is often mentioned in the literature (McAtee 1940, Kessel 1957, Hilton 1958), its function remains unclear. Perhaps the waving of greens by a male is a way of increasing his signaling ability, announcing nest ownership. Its presence in the nest box may be an important stimulus to the female to engage in nest-building.

Intrusion by one bird into the domain of another often led to aggressive threats. Sometimes the encounters resulted in direct attack, with the combatants grappling to the ground. Although Ellis (1966) stated that severe encounters occurred among captive male Starlings, no description of the actual contact was given. Hilton (1958), however, mentioned contact fights between Starlings.

In the low-density cages of this study, 11 deaths occurred from the time the birds were released in their cages to the end of May (table 1). All nine males died between 20 January and 19 March. Seven apparently died as a result of wounds inflicted in aggressive encounters, as evidenced by the massive hematomas on the posterior portions of the skull and neck. With effective escape in captivity precluded as a buffer to aggression, persistent chases took place. Using its feet, a dominant bird grasped a subordinate by the wings and

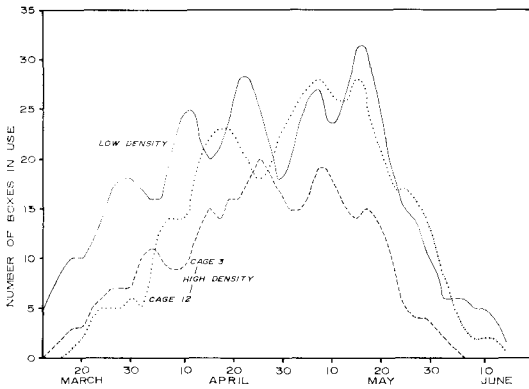


FIGURE 3. Box utilization by captive Starlings in the combined low-density cages and in two high-density cages based on 3-day moving averages.

pinned it to the ground, repeatedly pecking the head and twisting the skin.

Occasional vicious fights were noted early in the season in boxes of the high density cages, but no deaths occurred. This may be explained by the fact that persistent pursuit of an individual was hindered by interference from many birds at high density. Davis (1959) found that, in captivity, two males and two females established a definite social rank in which the males were dominant. The results reported here suggest that a hierarchy forms among low-density caged birds whereas no clear-cut dominance relationships develop at high-density.

BOX UTILIZATION AND EGG-LAYING

The number of boxes in use throughout the season in high- and low-density cages is plotted in figure 3. Utilization was significantly greater on the average, by date, in Cage 12

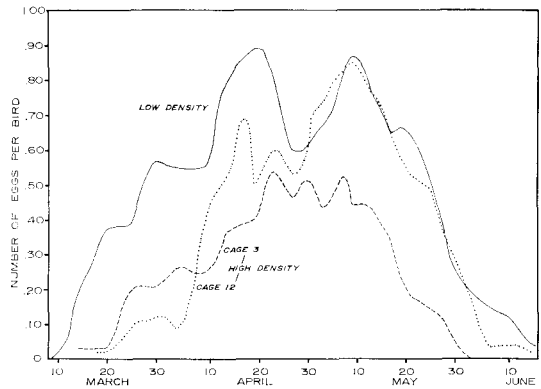


FIGURE 4. Eggs/bird ratios for captive Starlings in combined low-density cages and in two high-density cages based on 3-day moving averages.

than in Cage 3 ($P < 0.05$). However, there was no significant difference in usage when the low-density cage data were combined and compared with the combined high-density cages.

To compare rates of egg-laying, eggs/bird ratios by date for low- and high-density cages were plotted in figure 4. Egg-laying rates at high density lagged considerably behind those in low density, but the two high-density cages differed unexpectedly from one another. In Cage 3, peak eggs/bird ratio was achieved from about 25 April to 8 May while in Cage 12, two peaks of greater magnitude occurred about 17 April and 10 May. The following analysis of reproductive performance, therefore, compares not only the combined low- and combined high-density cages but also compares the performance in the two high-density cages separately (table 2).

TABLE 2. Comparison of reproductive performance in captive Starlings.

	Combined low-density cages ^a	Combined high-density cages ^b	P^c	High-density cage 3	High-density cage 12	P^c
No. boxes utilized	46 (92)	81	NS ^f	36	45	< 0.05
Percent potential pairs actually breeding	0.92	0.81	—	0.72	0.90	—
Total no. clutches ^d	93 (186)	132	< 0.001	57	75	< 0.001
Mean no. clutches per breeding pair	2.0	1.6	< 0.001	1.5	1.6	NS
Total eggs laid ^d	386 (772)	459	< 0.001	196	263	< 0.01
Mean clutch size ^e	4.2	3.8	< 0.001	3.7	3.8	NS
Total clutches aborted	13 (26)	32	NS	14	18	NS
Percent clutches aborted	0.13	0.24	—	0.24	0.24	—
Percent hatchability	0.70	0.76	NS	0.75	0.76	NS
Mean days young survive	3.5	3.1	< 0.01	3.1	3.0	NS

^a Five cages with 10 pairs per cage, 100 birds total; doubled value in parentheses.

^b Two cages with 50 pairs per cage, 200 birds total.

^c Significant difference determined by t -test for mean values; chi-square for total values.

^d Includes aborted clutches.

^e Excludes aborted clutches.

^f NS = Not significant.

TABLE 3. Comparison of all successful clutches laid by captive Starlings at low and high densities.

	1st Clutch		2nd Clutch		3rd Clutch	
	Low ^a	High ^b	Low	High	Low	High
N	43	68	24	28	9	4
Mean no. eggs per clutch	4.2	3.6 ^c	4.1	4.1	4.3	4.3
Percent hatchability	0.75	0.81	0.70	0.70	0.66	0.66

^a Five low-density cages combined.

^b Two high-density cages combined.

^c Difference between means significant, $P < 0.001$, by *t*-test.

Corresponding to the higher box utilization in Cage 12 there was a significantly greater total number of clutches in 12 than in Cage 3 ($P < 0.001$). The number of clutches was also greater in the combined low- than in the combined high-density cages ($P < 0.001$). When mean number of clutches per breeding pair and the overall mean clutch size for the two high-density cages were compared with each other, no significant differences were noted. However, mean number of clutches laid and overall mean clutch size were significantly greater in combined low-density cages than in the combined high-density cages ($P < 0.001$).

It was hypothesized that differences in amount of egg-laying at low and high density could be explained in terms of nesting-site arrangement. Compartments in the colony boxes of Cage 3 were separated only by partitions, whereas the boxes in Cage 12 were spatially separate. The average distance between the entrances to nest sites in Cages 3 and 12, excluding corner boxes and spaces between colony boxes, was 18 cm and 28 cm, respectively. The average distance between boxes in low-density cages was 140 cm. Perhaps as the distance between boxes increases, the proclivity for adjacent nesting in high-density cages also increases. In order to test this hypothesis, a score of 1 was assigned when two adjacent sites were in use, 2 when three adjacent sites were in use, and so forth. The total score for each high-density cage, recorded on alternate days throughout the breeding season, was subjected to the *t*-test, which showed the difference to be highly significant ($P < 0.001$). The propensity to occupy adjacent nest sites when spatially separated therefore accounts for the greater number of eggs laid in Cage 12.

A Starling's territory normally consists of that area within a 25–50 cm radius around the cavity entrance (Kessel 1957; Hilton 1958). Under crowded conditions, this territory can apparently be compressed further. The results reported here indicate that there is a limit to how close neighbors will be tolerated, although some individuals are more tolerant than others.

Table 3 shows that mean clutch size for all

first clutches in low-density cages was significantly greater than in the combined high-density cages ($P < 0.001$). This was not true, however, for subsequent clutches, which were equal in size. The largest clutch laid in captivity contained seven eggs.

HATCHABILITY AND YOUNG SURVIVAL

No significant difference in percent hatchability existed between low and high density (table 2), but young survived longer at low density ($P < 0.01$), probably because less competition for insect food that came into the cages allowed some insects to be taken to nestlings.

INTERVAL BETWEEN LAYINGS AND NEST ABANDONMENT

The interval between laying of successful clutches ranged from 4 to 19 days with a mean of 8.7 days for low density, and from 5 to 10 days with a mean of 7.5 days at high density. There is no statistically significant difference between these means.

Adult Starlings generally were not handled while in their nest boxes. Most Starlings vacated the boxes when the cages were entered for inspection. Out of the 10 instances where adults were frightened from a nest containing eggs, in only two was the nest abandoned completely.

DATES OF EGG-LAYING

The earliest egg of any clutch laid in captivity in 1969 was laid on 7 March in a low-density cage. Twenty-three days later, on 30 March, the first egg was laid in a nest box in the wild. The laying dates for all clutches in captivity contrast with the apparently synchronous laying that occurs in the wild (fig. 5).

Baker (1938) concluded that "as one goes north from the temperate latitudes one finds a general tendency for the egg laying seasons of birds of all kinds to start later and later at the rate of some 20 to 30 days for 10° latitude." No comparisons of the relationships among latitude, temperature, and date of egg-laying in Starlings have been made for western North

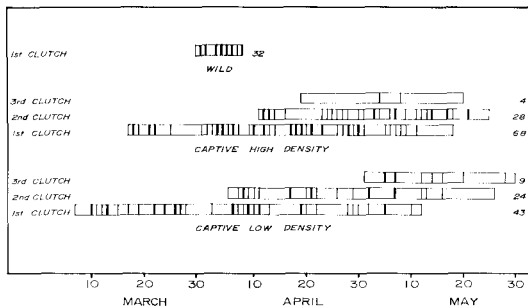


FIGURE 5. Range of laying dates for first eggs of clutches laid in captivity (1969) and in wild Starlings nesting near the aviaries (1964-69). Vertical lines within bars represent date on which first egg of clutch was laid. Thicker lines represent more than one clutch. Sample size is to the right of each bar.

America, but it is known that the cline of egg-laying dates in eastern North America closely parallels the latitudinal lines east of the 95° meridian line. At any given locality, Starlings in a population will begin egg-laying each year within three or four days of each other. The uniformity of this behavior, stated Kessel (1957), "indicates that wide-spread environmental factors such as light or local climatic conditions must largely determine time of egg-laying." She concluded that while day-length appears to be the primary environmental factor influencing gametogenesis in Starlings, the annual variations in egg-laying in a given locality are apparently caused by differences in temperature.

While this explanation may account for variations in egg-laying among wild birds in a given locality, it does not account for the striking difference between captive and wild Starlings living under essentially the same environmental conditions. Captive Starlings began egg laying 23 days earlier than the wild population in 1968 during the preliminary experiment and again in 1969.

Starlings in captivity were closer to potential mates than were wild Starlings, thus minimizing the distance and time for mate attraction. The presence of nest boxes reduced the amount of time spent exploring and competing interspecifically for a breeding site. With food constantly available, an important environmental pressure was relaxed. A constant supply of nesting material minimized the amount of time spent searching for this item. Also, predation in captivity was eliminated. Thus, with all breeding requirements more readily available to captives, and many individuals displaying in close proximity to each other, social stimulation was a relevant external force acting on the cycle, and may have led to an

early initiation of breeding by some individuals in the captive population.

DISCUSSION

Starlings in this experiment were living in a climatic environment nearly identical to that of the wild population. The densities established, however, were considerably greater than are normally found in nature. The primary purpose of the study was to ascertain the responses to high population density. The effect on reproductive performance was evident in the greater number of clutches and larger mean clutch size of low-density caged birds (table 2). This agrees with Lack's (1966) field data demonstrating a larger clutch size at lower densities in the Great Tit (*Parus major*).

Theoretically, if available space in each cage was equally divided among the occupants, each pair of Starlings in a high-density cage would occupy about 0.75 m³ while each pair in a low-density cage would occupy 3.78 m³. Based on the total number of eggs laid in high- and low-density cages (table 2), each pair produced 4.5 and 7.7 eggs, respectively. Thus, in high-density cages, a pair of Starlings produced six eggs per unit of space available to them and in low-density cages each pair produced about two eggs per unit of space. Clearly, if egg production were the primary objective, on an egg per unit space per pair basis, it would be economically advantageous to crowd birds.

For 32 first clutches of Starlings nesting in the wild in the Davis study area between 1964 and 1969, the mean clutch size was 5.0 with 91% of the eggs hatching. This is somewhat higher than mean clutch size for captive Starlings in this experiment.

A distinct latitudinal variation exists in the mean first clutch size in North American Starlings. Arizona Starlings averaged 4.5 eggs (Royall 1966). For Starlings nesting at Ithaca, New York (Kessel 1957) and Guelph, Ontario (Collins and DeVos 1966), mean first clutch sizes were 5.5 and 5.6 per clutch, respectively. That these variations may be attributable to environmental factors cannot be overlooked. It is Lack's theory that birds can find more food for their young at higher than lower latitude. In this study, birds in captivity laid first clutches which were somewhat smaller in size than those in the wild. Nutritional requirements necessary to prepare wild birds physiologically for the breeding season are poorly understood. High protein food in the form of dry pellets was continually available to captives, and may have been partially responsible

for the earlier initiation of egg-laying. It may be that even though there was an abundance of food, thus reducing competition for this resource, the quality was insufficient for maximum egg production. In the wild population, breeding may have been delayed to correspond with the availability of a particular food source of suitable quality not only for females to produce the maximum number of eggs but also to feed their young.

It has been suggested that the reduction in the average clutch size in late nestings as compared to early ones is advantageous because the food supply is less for nestlings later in the season (Lack 1948). Table 3 shows that rather than decreasing clutch size, subsequent clutches in captive Starlings increased slightly. It is hypothesized that since captive broods did not survive to fledging, the females were able to respond with a greater physiological effort. It is also possible that constant food supply was responsible for no reduction in clutch size. Survival of young Starlings under captive conditions, which may be possible when adults are provided with the proper diet that can be taken to their young, will permit this hypothesis and others related to food supply and population regulation to be tested experimentally.

It is generally accepted that the prerequisite to securing a mate is nest-site ownership. In natural populations of hole-nesting birds, the behavioral characteristic limiting breeding densities is territory (von Haartman 1957). In high-density Cage 3, defense of fewer nest boxes and, correspondingly, formation of fewer pairs (table 2) were explained by nest-site arrangement. It appears that territorial interference occurs when entrances to sites are within 18 cm of each other. Those individuals that did breed, however, demonstrated a mutual tolerance, allowing constriction of territories. Starlings are not considered social breeders, yet they are highly social during part of their annual cycle. In certain newly exploited habitats such as the southwestern United States, one might speculate that selection would favor a species that is inter-specifically aggressive, but flexible enough to tolerate conspecifics nesting within a close distance. That this may occur in nature is illustrated by the effective utilization of palm fronds and sahuaro cacti for breeding sites by many pairs of Starlings (Banks 1965; Royall 1966). Some species of the family Sturnidae are, in fact, social nesters (Lack 1968), and constriction of nesting territories may well have been an initial step in the evolution of communal nesting behavior (Crook 1965).

Recently, it has been reported (Victoria and Collias 1973) that the highly colonial African Village Weaverbirds (*Ploceus cucullatus cucullatus*) will initiate breeding earlier, have a larger clutch size, and experience a prolonged breeding period when crowded. But this will vary depending on the time of the breeding season that experimental crowding is induced. Although eventual social nesting by the European Starling is unlikely, the captive population demonstrated a remarkable adaptability to unusual nesting conditions.

Population regulation, in broad terms, is a complex interaction of behaviorally stimulated physiological responses to existing environmental conditions. In order to make clear the underlying mechanisms, it will be necessary to analyze experimentally those phenomena in natural populations which appear to function in regulatory roles. Such an approach, in which pertinent variables can be controlled, permits these interactions to be examined more closely.

SUMMARY

The hypothesis that high population density can modify reproductive effort in a wild species was tested experimentally. Captive Starlings were caged at different densities under natural light and temperature conditions and provided with the following requisites for breeding: (1) nest boxes; (2) enough space for an aerial chase; and (3) nesting material including some green vegetation. Behavioral and physiological responses, particularly egg-laying, were emphasized.

Densities of 10 pairs and 50 pairs demonstrated that birds at low density laid more eggs than those at high density. This is the result of more clutches per pair and larger mean clutch size at low density. Differences that prevailed in these parameters in the two high density cages were explained by unequal nesting-site arrangement.

A comparison of first egg deposition showed that captive Starlings at both densities were initiating egg-laying as much as three weeks earlier than wild Starlings nesting in the same vicinity. Proximity of captives to nest sites and material, potential mates, and food resources may minimize certain reproductive preliminaries and account for this temporal difference.

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