POPULATION DYNAMICS OF THE CATTLE EGRET

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INTRODUCTION

The colonisation of South Africa by the Cattle Egret *Ardeola ibis* and the bird's increase and spread in the country since the beginning of the present century have been documented by Skead (1952) and Siegfried (1965, 1966b). This report deals with an examination into *A. ibis*' rate of population build-up in relation to its reproductive output and mortality.

POPULATION DYNAMICS

The number of animals recruited to a population and surviving to breed must equal the average annual mortality in adults in order for the population to remain stable. For *A. ibis*, mortality rates of populations in South Africa have been computed by Siegfried (1970), and data on the species' productivity are available as well (Siegfried in press).

In the south-western Cape Province mortality-rates in adult and first-year Cattle Egrets are 23 and 35 per cent respectively. Assuming that all Cattle Egrets attempt to breed at the end of their first year (which seems to be a valid enough concept when applied to the south-western Cape (Siegfried 1966c and unpublished), then it is necessary for each pair of breeding birds to raise 0,71 young to replace the 23 adults dying that year. Similarly for the sub-continental population, which has mortality-rates of 37 per cent for first-year birds and 25 per cent for older birds, each pair of breeders would have to produce 0,79 young to independence in order to maintain stability in the population. These calculations are based on the equation:

$$r = \frac{2M_A}{1 - M_J}$$

where r = number of chicks per breeding pair
M_A = adult mortality
M_J = juvenile mortality.

Reproductive output of *A. ibis* in the south-western Cape averages about one chick, raised to full independence, per breeding pair per annum (Siegfried, in press). This output is, on average, slightly above the level required to maintain a stable population. From this, it might be inferred (if the data on survival of first-years and adults are not biased) that the region's *A. ibis* population is increasing slightly, which would accord with the known facts on its recent history. Data on breeding success in other parts of South Africa are not available, but I expect that breeding occurring in man-modified habitat generally is unlikely to be much more productive than in the south-western Cape.

Assuming for the moment that deferred breeding might operate generally in saturated

A. ibis populations, and that all Cattle.Egrets first breed at two years of age, and that mortality-rates of 37 and 25 per cent apply to first-year and older birds respectively, then, it will be necessary for each pair of breeders, if all second-year and older birds breed once a year, to raise an average of 1,1 young to fledging to replace the number of adults dying that year. The equation for this is:

$$r = \frac{2M_A}{(1 - M_J)(1 - M_A)}$$

Turning now to *A. ibis*' history, and its rate of colonisation and spread as a breeding bird in South Africa, it is instructive to examine these factors in relation to the species' reproductive output. Absolute data on the numerical strength of the population, and its rate of build-up, are available only for the Cape Province and even here, it must be stressed, the figures are, at best, crude estimates. Nevertheless, for purposes of rough comparison, it can be stated that in the south-western Cape the *A. ibis* population had increased from 1 000 birds in 1930 to 30 000 in 1960. For the Cape Province as a whole (an area of 277 000 sq. miles), the population had increased from 1 000 in 1910 to 100 000 in 1960 (Siegfried 1965, 1966a).

In *A. ibis* an average clutch size of three eggs can be regarded as representative of the southern African population (and probably of all populations). If we assume that the average number of eggs in a clutch has been evolved to correspond with that from which, on average, most young are raised (Lack 1954, 1966), and that the average theoretical maximum reproductive output per breeding pair is three young per annum, then this statistic can be used to construct a theoretical dynamic population model. Applying the average mortality rates of 37 per cent (first-years) and 25 per cent (adults), it emerges that the model population is capable of increasing at the rate of 70 per cent. The workings supporting this are as follows:

$$N_{t+n} = N_t \left(S_A + \frac{rS}{2} J \right)^n$$

where N_t = population number at time t.
S_A = survival of adults
S_J = survival of juveniles

If a second model be constructed employing a productivity rate of 1,0 young per breeding pair per annum (which is close to that measured in the south-western Cape), then the rate of increase each year drops to 6,5 per cent. At this cumulative rate of growth, 73 years and not 50 would have been needed for the population to have increased from 1 000 to 100 000 individuals in the Cape Province. Similarly, in the south-western Cape (9,5% increase) 38 years and not 30 would have had to elapse to reach a population of 30 000 birds.

DISCUSSION

The significance of the above extrapolations is, of course, speculative, but the point I wanted brought out is that, it is unlikely that the South African *A. ibis* population, breeding as it does almost exclusively in extensively man-modified habitat, would alone have been able to sustain the relatively sudden and rapid build-up in numbers throughout the country during the past half-century, and especially the last 30 years. Thus, it appears that part of the "population explosion" was, and still is, due to regular, both permanent and temporary, immigration from elsewhere.

The interpretation offered here is that *A. ibis*' ancestral breeding grounds, and also its modern ones in undisturbed natural regions, supported food resources whose ecological availability was considerably better than those in most man-modified habitats. The crucial point in this reasoning is that, the man-made habitats do not provide sufficient quantities of suitable food at a rate sufficient for the full potential of the species' reproductive effort to be realised; and, the species' average clutch-size in these areas is maladaptive when viewed in relation to the average number of young raised.

The effect of this deficiency is revealed at the peak of the chick-rearing phase in the nesting cycle. Thus, productivity in man-modified habitat is lowered mainly by a reduction of actual chicks through starvation; and not, theoretically at least, through egg-loss and size of breeding population. In short, in man-modified habitat, quantity and quality of food supplied at the beginning of the breeding season permit a population to breed which, in size and in number of eggs produced, will yield more chicks than the parents can adequately nourish and raise. At the pith of this explanation is the supposition that it is not the overall biomass of the food resources which is important, but rather the ecological availability of food which influences the parents' energy-budget (Siegfried in press).

Advancing the above hypothesis, one might speculate that a relatively improved realisation of the species' reproductive potential has always prevailed in natural areas. In fact, one might say that if the species' low mortality-rate is real, then population turn-over in the natural areas has always resulted in a considerable surplus of birds. A regular surplus would presumably promote regular dispersal, and it is apparently this phenomenon which lies at the heart of *A. ibis*' spread into, and colonisation of, South Africa and also other regions. The fact that its spread has been so recent (i.e., the last 50 years or so) does not alter the argument: while dispersal has presumably always occurred, it is only recently that ecologically suitable habitats have been extensively created by man in areas which formerly provided habitat either unsuitable or marginal for *A. ibis*. It is suggested that it was only once relatively large-scale land-reform had taken place that conditions were suitable for *A. ibis* to have established viable resident populations (Siegfried 1965, in prep.). The reasoning that breeding effort in *A. ibis* in natural areas has always been far more productive than might be required to maintain stable levels in populations, and that a large surplus of birds results, accords with Lack's (1966) view that a species has evolved those adaptations which permit it to reproduce as rapidly as it can in its natural habitat. In short, it is suggested that breeding by *A. ibis* in natural habitat, on average, results in over-population with consequent dispersal. Even if the species should only breed for the first time when two years old, its theoretical output should still ensure a considerable surplus.

Finally, the ideas advanced above require further testing by investigating the success and productivity of *A. ibis* populations breeding in man-modified habitat outside the south-western Cape, and especially in natural habitat in undisturbed areas. Also, once a sufficient period of time has elapsed, the mortality rates (Siegfried 1970) require to be re-examined.

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SUMMARY

The paper reports an examination into the Cattle Egret's, *Ardeola ibis*, population build-up in South Africa in relation to its reproductive output and mortality. In man-made habitat the observed reproductive output, although apparently much lower than the theoretical one at which the species is adapted to reproduce, is still sufficient to maintain a stable population. However, it is claimed that this relatively small surplus alone could not have accounted for the rapid rate of build-up of the South African population. It is postulated that immigrant Cattle Egrets, arriving as a result of dispersal of a surplus produced by populations breeding in natural undisturbed habitat, have served to advance the species' "population explosion" in man-made habitats in South Africa.

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