Kirtland's W
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COWBIRD-HOST INTERACTIONS

Brood parasitism, a frequency dependent homeostatic mechanism may negate Gause's principle in the field.

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Since the equilibrium pressure-frequency area is identified, and apparently is also the point for a stable population and the point at which the supra optimal system is operating with the good hosts' population in nature, it is assumed the good host-cowbird interaction is indeed in equilibrium. Empirical knowledge of the stability of parasitized populations, at least before the advent of pesticides, supports this reasoning. But perhaps more direct evidence is now available on the dynamics of this delicately balanced system.

Consider the Kirtland's Warbler data from the 1951 and 1961 censuses along with Mayfield's most valuable data on parasitism, 7 years of which were taken during that period. Although less than ideal (not covering the total period) these data would still seem to be the final, convincing quantitative evidence, from total population counts, which are needed for acceptance of the equilibrium hypothesis for cowbird parasitism. This relict, endangered population was apparently under less than 72 equilibrium cowbird pressure (58) and frequency (24). Its population apparently increased accordingly (16 percent in 10 years)[36], as is predicted by these patterns. The 1971 census by contrasts revealed a 60% decrease in numbers [37]. Evaluation of recent data on control (unmanaged for cowbird) areas[38] reveals a supra equilibrium pressure of 78.5, (32 frequency) as expected.

Summary

The cowbird-host interaction is investigated quantitatively and qualitatively by means of a density or frequency dependent pressure index. This index is the mean of the precent frequency of parasitism on hosts (incidence of nests parasitized) and the precent frequency of multiple eggs with respect to total cowbird eggs (intensity of parasitism).

Cowbird and host fledging success and losses to parasited correlate with the pressure index. Small hosts being vulnerable to competition for heat, food, and care with cowbird eggs or nestling are intolerant, give a low fledging success to the parasites and are rated poor hosts. Larger hosts being less vulnerable, are more tolerant, accept more eggs, raise more cowbird young and are rated good hosts.

The system of analysis is apparently accurate, assuming adequate sampling and the steady state. It is apparently predictive and has merit. Rigorous statistical tests reinforce the belief these are true population patterns.

Since good and poor host success and losses to cowbirds and cowbird success with each are apparently functions of cowbird pressure, algebraic formulae for same are presented.

Host egg size may be the simplest indicator of type of host encountered when same is inknown, since it has a direct bearing on ability to compete with the cowbird egg or young for heat, food, care, etc..

The Kirtland's Warbler is apparently not in the danger suspected from the cowbird. Egg size predicts this large warbler should be in the good host group. Also with all other hosts acceptance of a high cowbird multiple egg burdenand raising of a good portion of same to fledging indicates an ability to endure this parasitism without undue losses to their own population potential. The 1961 census also did not reveal the expected decline.

Critical examination reveals the apparent criteria for sampling used in the 1960 report was complete knowledge of total history of nests from egg laying through termination, successful or otherwise. When what seems to be the total nest sampling available is utilized in the traditional fashion, with the added insights now provided by the parasite pressure-density or frequency reference frame, a balanced interaction pattern comparable to that of other good (less-susceptible) hosts is apparently established.

The patterns indicate the cowbird is density, or more accurately with this approach, frequency dependent, with some 22 species of two types of hosts. Frequency dependency is a prerequisted for a stable equilibrium. Cowbird pressure is dependent upon and can be translated into cowbird frequency relative to host numbers with a ratio of four cowbird females per 100 pair of hosts for each 10 units of pressure.

The finding of the equilibrium point, stable population frequency area and operation of this system in nature at the same 72 pressure - 28 frequency area, would seem ample evidence that the total supra- optimum, good host-cowbird interaction is indeed in equilibrium.

The Kirtland's Warbler population under less than this equilibrium pressure apparently increased, under greater than 72 pressure, decreased as these patterns predict. This may be the needed field evidence matching recent lab evidence to negate Gause's principle of competitive exclusion in these frequency dependent circumstances where relative competitive fitnesses are inversely proportional to the relative frequencies of the two species competing for the same limited resources.

Conclusion

Cowbird parasitism in theory and operation apparently fulfills the requirements for an equilibrium interaction. As first reported in 1958, and subsequently it is apparently a homeostatic mechanism.[39] These, by acting upon doomed or unneeded surpluses, tend to stabilize rather than harm populations by keeping them in line with amount of optimal habitat thus preventing violent oscillations.[40] Therefore, under natural conditions, they must be considered beneficial.

from Tables 33, 34, 35: p.p. 189, 190, 191, Mayfield 1960

	Unp. Nests: Number Nests	Unp. Nests: Number K.W. fledged	P. Nests: Number Nests	P. Nests: Number K.W. fledged	P. Nests: Number C. fledged
Table 33 Unsuccessful Nests	21	0	16	0	0
Table 34 " "	7	0	10	0	0
" " " "	3(omitted)	0	11(omitted)	0	0
" " Successful "	28	104	17	25	19
Table 35 " "	42	164	27	27	39
Totals	101	268	81	52	53

Total K.W. eggs laid in 101 Unp. nests X 4.63 (*) = 468 eggs and 268 fledged = 57.3%

" " " " " 81 P. nests X 4.63 = 375 " " 52 " = 13.9%

Success difference = loss to cowbirds = 43.4% of 375 eggs laid in the 81 parasitized nests = 163 eggs, and 163 eggs = 19.3% of the total 843 eggs laid by the K.W. in all nests.

Total eggs laid =843 Tot. succ. = 320

Total success of K.W. was 320 of 843 = 38% + 19.3% loss to C=57.3% of production accounted for as in non-parasitized segment.

Cowbird Data; 182 nests, 81 parasitized = 44.5% incidence. Table 21,: 148 gives 125 cowbird eggs (36 singles, 39 multiples = 71.4% intensity) in 75 parasitized nests. By calculation using 1.66 C eggs per parasitized nest we may add 10 more eggs to this number for our 6 more nests in this 81 nest sample. The ratio of multiples would be the same - 71.4%.

Therefore from 135 cowbird eggs in 81 parasitized nests of 182 nests total, 58 cowbirds fledged = 43% at a pressure of $\frac{44.5+71.4}{2}$ = 58. So the total picture is at a pressure of 58 the K.W. gained 38% success, the cowbird 43%, losses to cowbirds were 19.3%.

(*) Page 85, Paragraph 1 gives 4.63 as clutch size from 67 unparasitized nests whose clutches were complete.

on Dr. Van. ... paper on Cowbird Host Relationships for AUK 1972

Summary

Based on data collected in Pontiac, Oakland County, Michigan, and on published material on cowbird-host relationships, steady state conditions and adequate sampling apparently give about a 60 percent host fledging success and about a 40 percent loss to universal or nonspecific hazards without cowbird brood parasitism. This universal loss of 40 percent is also skimmed off the top of host and cowbird production alike in parasitized nests under similiar conditions.

A single pressure index figure dependent upon and reflecting cowbird brooding female density is achieved by averaging two equally important phases of the parasite pressure complex upon the host population, the incidence or percent of nests parasitized and the intensity of parasitism those nests are subject to, as measured by the percent of total cowbird eggs deposited that are laid as multiples - two's, three's, four's, etc. in a nest, as distinguished from the singles.

This pressure index, dependent upon and reflecting cowbird density with respect to available hosts, correlates with host losses to cowbird in a manner consistent with theory.

If sampling is adequate and a steady state exists (the system is in equilibrium), host and cowbird success can also be correlated with cowbird pressures also in a manner consistent with theory.

Host data can thus be plotted against this horizontal pressure line (X axis) from two different aspects, counting up from below on the left (Y axis) for the successes and down from the 60 percent steady state success base line for losses to cowbirds on the right vertical axis.

In cases where the system is in a steady state of equilibrium and sampling has been adequate, both approaches agree. In cases where sampling is small and/or no equilibrium or steady state exists, (as when the habitat has

undergone extreme change from weather, or man), the success data cannot be depend-ed upon to furnish a pattern. The losses to parasites then may give the most reliable data, if accurately ascertained. If host success data are off expect-ation level because of variation in the steady state, then cowbird success data will also be off the expected area in the same direction. A cause-effect devi-ation can also be recognized to minimize confusion. This is, in essence, re-cognition of the fact that the cowbird sampling is often small enough to be swayed from success expectation by chance, but being a partial determinator of host success, it then sways host success in an opposite and reciprocal fashion from steady state expectation.

As pressures are dependent upon and reflect parasite density these data also determine that cowbird success is density dependent with these two hosts. Its success illustrates Allee's principle which states a suboptimum density can be as limiting as a supra optimum density for a species. A definite but dif-fering optimum pressure area for each of these two hosts, can be pinpointed, of interest for evolutionary studies.

The Yellow Warbler is a poor host, giving a low maximum fledging success of 18 percent to the cowbird even at a low optimum pressure (30). The Song Sparrow is a good host, giving a higher 42 percent success to the cowbird at 60 pressure, twice the poor host optimum, while a 54 percent maximum success is possible at an optimum pressure of 50. An 18 percent host loss is incur-red by both these hosts at these widely different parasite pressures of 30 and 60, demonstrating their differing susceptibilities. These varying sus-ceptibilities control, via feedback in this natural density dependent system, the different successes of the parasites at the various pressures. Host sus-ceptibilities, therefore intolerances honed by evolution, apparently set limits on acceptable cowbird interferences and pressures and therefore densities. In-traspecific competition also depresses cowbird success above optimum density.

Two factors, therefore apparently determine cowbird fledging success, first, choice of host, and second, parasite pressure via density with reference to host numbers. Their sccess can vary from ... at the extremes of pressure (and density) to 18 percen at the optimum with the poor host, Yellow Warbler, and 54 percent at the optimm with the good host Song Sparrow: but it seemingly averages less than 42 ercent with this god host as they apparently usually level off at a higher than optimum denity coinciding with the 60 to 70 pressure area according to later data. Th preceding two symmetrical and balanced interaction patterns ith parasite otimums at different pressure levels in each, are suggestive eidence, supported by what rigor is inherent in the negatively oriented Chi-square test, that brood parasitism on these two species is apparently a well regulated homeostatic mechanism.