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COMMENTARY

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MEASURING ANNUAL REPRODUCTIVE SUCCESS IN BIRDS¹

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Abstract. From simulated data on three populations, I calculate different measures of “reproductive success”: clutch size, egg success (the proportion of eggs that produce young), nest success (the proportion of clutches that produce young), and the annual reproductive success per female in terms of both number of broods and number of young reared successfully during a breeding season. These measures of success are not correlated. Differences in egg success or nest success do not necessarily translate into differences in annual reproductive success, and differences in annual reproductive success do not necessarily translate into evolutionary success.

Key words: broods, clutch size, clutch size equation, egg success, nest success.

Ornithologists studying reproductive success usually report the percentage of eggs or nests in a population sample that is successful in producing young. “Egg success” is the percentage of eggs that produce young that leave the nest. “Nest success” is the percentage of nests with eggs that produce young that leave the nest. These measures of success are often compared among species living at different latitudes, in different habitats, or in different nest types (Lack 1968, Ricklefs 1969, Skutch 1985).

Sometimes ornithologists calculate annual reproductive success (ARS) in order to calculate lifetime reproductive success (LRS). ARS and LRS may be calculated in terms of the mean number of young fledged or yearlings produced by the reproducing females (Clutton-Brock 1988, Newton 1989), depending on the data available or the interests of the investigator.

As Rowley and Russell (1991) correctly pointed out, “. . . the figure of demographic significance is the number of fledglings produced per female each year (FFY) and this figure is remarkably difficult to extract from the literature.” Individual males and females, not nests or eggs, are the reproducing units on which natural selection acts. With regard to the evolution of traits, what matters is how well the individuals with a trait (say, red eyes) do with respect to individuals with alternative traits (white eyes), providing those traits reflect genotypic differences (Murray 1990, 1995, 1997). Nest success and egg success are only two factors af-

fecting reproductive success, and reproductive success is only one of several factors affecting the evolutionary success of a trait or genotype.

In this paper I calculate and compare the various measures of “success” from simulated data.

METHODS

In order to compare the various methods of measuring “reproductive” success, I simulated data for three populations, A, B, and C (Table 1). With these data, I calculated egg success and nest success for each population with the standard method (Nice 1957, Ricklefs 1969, Skutch 1985). Thus,

$$\begin{aligned} \text{egg success} \\ &= \frac{\text{number of young that leave the nests}}{\text{total number of eggs}} \end{aligned} \quad (1)$$

$$\begin{aligned} \text{nest success} \\ &= \frac{\text{number of clutches that produce young}}{\text{total number of clutches}} \end{aligned} \quad (2)$$

What ornithologists almost never calculate is the mean reproductive success of the females of each population (Murray 1991a, Rowley and Russell 1991). I have proposed that ornithologists should calculate the mean reproductive success of the females of a population in terms of both the number of broods and the number of young reared successfully through independence (if data are available) or nest leaving (Murray et al. 1989, Murray 1991a). The best demographic indicator of a group of females is the ARS of all females of breeding age, including the nonbreeders (Murray 1991a), which is not, however, the ARS of Clutton-Brock (1988) and Newton (1989). If such data are unavailable, the next best indicator is the ARS of the population of sampled females. An investigator should note whether his or her calculated ARS includes the unmated females of reproductive age.

The annual reproductive success (ARS) of a population of females (counted as the number of broods successfully reared per female) is measured with one version or another (depending on the mating system) of the following general equation (Murray 1991a),

$$\text{ARS}(b) = c_1s_1 + c_2s_2 + \dots + c_ns_n \quad (3)$$

where c_1 , c_2 , and c_n are the number of clutches laid per female in producing the first, second, and n th broods, respectively, and s_1 , s_2 , and s_n are the probabilities of rearing any young from the first, second, and n th brood clutches, respectively. ARS (counted as the number of young successfully reared) is better measured with one version or another of,

$$\text{ARS}(k) = c_1s_1k_1 + c_2s_2k_2 + \dots + c_ns_nk_n \quad (4)$$

where k_1 , k_2 , and k_n are the mean number of young reared in successful first, second, and n th broods, respectively. The benefit of calculating reproductive success with these equations (or some version of them) is that ARS in different species and situations becomes directly comparable.

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TABLE 1. Reproductive success of three populations. Population A is multibrooded. Populations B and C are single brooded. In this table, for example, 70 females laid a first first-brood clutch of which 13 were successful. All 57 failed females laid a second first-brood clutch of which 9 were successful. Of the 13 successful females, 8 laid a second clutch (their first second-brood clutch), of which two were successful. In these examples all females of breeding age laid at least one clutch.

Clutch number in laying sequence	Number first-brood clutches	Number of successful broods	Total eggs	Total fledglings	Mean clutch size	Mean fledglings/successful brood
Population A: First-brood clutches						
1	70	13	287	47	4.10	3.62
2	57	9	222	30	3.89	3.33
3	43	13	163	42	3.79	3.23
4	23	10	85	31	3.70	3.10
5	7	3	23	9	3.28	3.00
6	2	1	6	3	3.00	3.00
7	1	0	3	0	3.00	—
Total	203	49	789	162	3.89	3.31
Population A: Second-brood clutches						
1	—	—	—	—	—	—
2	8	2	30	6	3.8	3.0
3	5	2	18	7	3.6	3.5
4	1	0	—	—	—	—
5	1	1	3	3	3.0	3.0
6	0	0	—	—	—	—
7	0	0	—	—	—	—
Total	15	5	51	16	3.4	3.2
Population B: Single-brooded						
1	86	30	418	91	4.86	3.03
2	56	25	242	101	4.32	4.04
3	25	12	85	25	3.40	2.08
Total	167	67	745	217	4.46	3.24
Population C: Single-brooded						
1	64	10	389	50	6.08	5.00
2	54	15	292	67	5.42	4.47
3	30	10	165	45	5.50	4.50
Total	146	35	846	162	5.79	4.63

RESULTS

In the simulations, the 70 females of population A laid a total of 840 eggs in 218 nests (mean clutch size, 3.85). Egg success is 178 fledglings/840 eggs or 0.21. Nest success in population A is 54 successful nests/218 nests with eggs, that is, 0.25. The number of fledglings produced per successful clutch is 3.30 (= 178/54).

The 86 females of population B laid a total of 745 eggs in 167 nests (mean clutch size, 4.46). Egg success is 217 fledglings/745 eggs or 0.29. Nest success in population B is 67 successful nests/167 nests with eggs, that is, 0.40. The number of fledglings produced per successful clutch is 3.24 (= 217/67).

The 64 females of population C laid a total of 846 eggs in 146 nests (mean clutch size, 5.79). Egg success is 162 fledglings/846 eggs or 0.19. Nest success in population C is 35 successful nests/146 nests with eggs, that is, 0.24. The number of fledglings produced per successful clutch is 4.63 (= 162/35).

The ARS (counted as mean number of broods reared) for the females of population A is (Eq. 3),

$$\begin{aligned} \text{ARS}(b) &= \left(\frac{203}{70}\right) \cdot \left(\frac{49}{203}\right) + \left(\frac{15}{70}\right) \cdot \left(\frac{5}{15}\right) \\ &= 0.700 + 0.0714 = 0.7714, \end{aligned}$$

for population B is,

$$\text{ARS}(b) = \left(\frac{167}{86}\right) \cdot \left(\frac{67}{167}\right) = 0.7791,$$

and for population C is,

$$\text{ARS}(b) = \left(\frac{146}{64}\right) \cdot \left(\frac{35}{146}\right) = 0.5469.$$

The ARS (counted as mean number of young reared, that is, the FFY of Rowell and Russell 1991) for the females of population A is (Eq. 4),

TABLE 2. Comparison of reproductive success indices of the three populations given in Table 1.

Population	Mean clutch size	Egg success	Nest success	Number of fledglings per successful nest	ARS(b)	ARS(k)
A						
first brood	3.89	0.21	0.24	3.31	—	—
second brood	3.40	0.31	0.33	3.20	—	—
total	3.85	0.21	0.25	3.30	0.7714	2.54
B	4.46	0.29	0.40	3.24	0.7791	2.52
C	5.79	0.19	0.24	4.63	0.5469	2.53

$$\begin{aligned} \text{ARS}(k) &= \left(\frac{203}{70}\right) \cdot \left(\frac{49}{203}\right) \cdot \left(\frac{162}{49}\right) \\ &\quad + \left(\frac{15}{70}\right) \cdot \left(\frac{5}{15}\right) \cdot \left(\frac{16}{5}\right) \\ &= 2.31 + 0.23 = 2.54, \end{aligned}$$

for population B is,

$$\text{ARS}(k) = \left(\frac{167}{86}\right) \cdot \left(\frac{67}{167}\right) \cdot \left(\frac{217}{67}\right) = 2.52,$$

and for population C is,

$$\text{ARS}(k) = \left(\frac{146}{64}\right) \cdot \left(\frac{35}{146}\right) \cdot \left(\frac{162}{35}\right) = 2.53.$$

These data are compared in Table 2.

It may seem obvious that ARS(b) or ARS(k) for population A could have been calculated without making the distinction between its first and second broods. ARS(b) is simply the number of broods reared divided by the number of females, and ARS(k) is the number of young reared divided by the number of females. I think that calculating ARS(b) and ARS(k) in this way loses important information, such as differences in success between first and later brood clutches. Although populations A, B, and C have virtually identical ARS(k), they each achieved this mean number of young reared per female in different ways.

DISCUSSION

The usual measures of reproductive success (i.e., egg success and nest success) appear to indicate that the females of population B are more successful than those of either population A or C. Twenty-nine percent of eggs of population B produced fledglings, whereas 21% and 19% of eggs produced fledglings in populations A and C, respectively. Forty percent of clutches of population B produced young to leave the nest, whereas 25% and 24% of clutches produced young in populations A and C, respectively. The mean clutch size (sometimes used as an indicator of reproductive success), however, is greatest in population C, 5.79, compared with 3.85 and 4.46 in populations A and B, respectively.

We might be tempted to conclude that the females of population B were more successful than those of either population A or C, and we might determine from

our study that the lower success in populations A and C was a result of, for example, the greater predation on nest contents, the greater difficulty the parents had in obtaining food for the nestlings, or to the rigors of the weather. Population A may live at lower latitudes (more predators), or in poorer quality habitat, or it may be an open nester, while population B is a cavity nester. We might also think that the females of population C are more successful than those of either A or B, even though they have the lowest egg and nest success, because they have bigger clutches.

The annual reproductive success in terms of number of broods reared [ARS(b)] is about the same in populations A and B, but smaller in population C. ARS(k), however, of the females of populations A, B, and C in these simulated populations is essentially the same (Table 2).

What are we to make of all this? First, determining which females have the greatest “reproductive success” on the basis of one of the usual measures (clutch size, egg success, nest success) could be misleading. Second, the mean annual reproductive success [either ARS(b) or ARS(k)] of the females of populations A and B is essentially unaffected by their differences in clutch size, mortality rate of eggs or nestlings, or number of young produced per successful clutch. The females of population A make up for their poorer nest success, from whatever cause, by laying more clutches and rearing second broods. Population C’s lower ARS(b) is offset by producing more fledglings per successful brood (k_i).

We certainly want to know whether differences in s_i (the probability that a brood i clutch is successful) and in k_i (the mean number of young produced from a brood i clutch) occur among populations, and we certainly want to know whether these differences result from predation on nest contents, available food supply, inclement weather, or some other factor. Nevertheless, we also want to know whether these differences affect the mean annual reproductive success [i.e., ARS(b) and ARS(k)] of females. In order to understand the dynamics of populations, we need to know more than the success of eggs or nests in producing young. If two populations differ in egg success or nest success but are each equally successful (sustaining their mean population size), we want to know what other factors balance these differences. The high mortality of clutches in the tropics, for example, is probably compensated for by females having long breeding seasons, allowing

the laying of more replacement clutches and often rearing two or more broods (Murray 1991b). Unfortunately, other than the fact that tropical passerines tend to lay more clutches and rear more broods than temperate zone species, quantitative comparative data are scarce (Cody 1971, von Haartman 1971, Ricklefs 1973).

Even differences in ARS and LRS of populations may be misinterpreted because the population (and, more specifically, genotype) with the greatest ARS or LRS is not necessarily the one favored by natural selection, that is, it is not necessarily increasing at a greater rate than populations with smaller ARS or LRS (Murray 1992, 1997).

Ornithologists have not yet started to measure c_b , s_b , or k_b , much less ARS(b) or ARS(k) in their life-history studies, despite my previous pleas for them to do so (Murray 1991a, 1994). In many studies, no doubt, investigators may not have the detailed information for making the calculations proposed here, but I am certain that the data are available in many of the life-history studies undertaken with populations of individually marked birds during the past two to three decades. Too much important information is being lost. Perhaps, this example will encourage ornithologists to include calculations of c_b , s_b , k_b , ARS(b), and ARS(k) in their studies.

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