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Corrections for the Underestimation of Brood Parasitism Frequency Derived from Daily Nest Inspections.—Intraspecific brood parasitism may be an important mode of reproduction in some species (Brown 1984, Emlen and Wrege 1986, Gowaty and Karlin 1984, Yom-Tov 1980). However, the frequency of intraspecific brood parasitism is difficult to measure because parasitic eggs are difficult to detect. Barring direct observations (Brown 1984, Emlen and Wrege 1986), or the use of electrophoretic identification techniques (Gowaty and Karlin 1984), researchers are often left to identify parasitic eggs through deviations from a normal egg laying schedule, from a larger than normal clutch size, or from contrasting intra-clutch egg coloration or measurements (Fetterolf and Blokpoel 1984, Yom-Tov 1980).

Of the latter methods, identifying deviations from a normal egg laying schedule is probably the most accurate. Two eggs appearing in a nest in the same day is unambiguous evidence of two females laying eggs in that nest (type 1). For alternate day layers, the appearance of one egg in a nest on each of two consecutive days (type 2) is less reliable evidence, since this could be explained by nest owners occasionally laying more often than expected. But if type 1 evidence is discovered along with type 2 evidence, the latter is quite likely to also be reliable evidence of brood parasitism (Frederick and Shields 1986).

However, even daily nest checks will consistently underestimate the frequency of brood parasitism because parasitic eggs laid one normal inter-egg interval before or after a host's clutch are indistinguishable to the observer from normally laid host eggs.

Here we present a simple method to conservatively correct this underestimation. For any specific clutch size, the probability of detecting a parasitic egg can be assigned as the number of theoretically detectable cases divided by the total number of possible cases. The number of cases actually discovered can then be corrected to a more realistic value by dividing it by the probability of detection.

Several important assumptions are necessary to enumerate the types of theoretical detections and the number of possible cases. We assume that all host species are determinant layers, that only one parasitic egg is laid in any clutch, that parasites do not remove host eggs as they parasitize, that parasitic eggs are equally likely to be laid on any given day of a host's egg laying schedule, and that the total period considered extends only one normal inter-egg interval before or after the host's egg laying period. Parasitic eggs appearing outside this time could not be confused with normally laid host eggs, and no correction is needed. Finally, we assume that evidence of both types 1 and 2 (above) is indicative of parasitic eggs in the case of alternate-day layers.

An example will be instructive. Under the above assumptions, if a host lays a total of three eggs on alternate days, there are nine different days on which one parasitic egg could be deposited. The parasitic egg is undetectable only when laid two days before the first host egg is laid, or two days following the host's last egg. Thus, the probability of detecting a randomly laid parasitic egg is 7/9, or 0.778 (see Table 1).

It should be noted that nearly all consistent mistakes due to the above assumptions would lead to conservative estimates of the frequency of intraspecific brood parasitism. The exception is the assumption that evidence of both types 1 and 2 are always indicative of a parasitic egg, which could lead to overestimation.

Probabilities of detection are presented in Table 1 for species that normally lay eggs every day and those that lay on alternate days. Note that daily nest checks underestimate

TABLE 1. Probabilities of detecting parasitic eggs using daily nest checks.

Total number of eggs in nest (host and parasite)	Eggs laid on alternate days		Eggs laid daily	
	Parasite does not remove egg	Parasite removes egg	Parasite does not remove egg	Parasite removes egg
2	0.600	0.143	0.333	0
3	0.714	0.111	0.500	0
4	0.778	0.091	0.600	0
5	0.818	0.077	0.667	0
6	0.846	0.067	0.714	0
7	0.867	0.059	0.750	0
8	0.882	0.053	0.778	0
9	0.895	0.048	0.800	0
10	0.905	0.044	0.818	0

the number of parasitic eggs by a considerable fraction in most cases. Probabilities of detection for alternate-day layers are higher because there is the added possibility of detecting parasitic eggs laid on the days between the laying of host eggs. For both types of layers, the probability of detection increases with clutch size.

The case is also considered where the parasitic female removes a host egg (if it is present) when she lays a parasitic one. It is necessary to assume that eggs are not marked in these cases, since the observer can rarely be sure whether a host or parasitic egg is being marked. If the host species lays eggs every day, parasitic eggs are never detectable. Similarly, if the host lays eggs on alternate days, a parasitic egg is only detectable if laid 1 d before the first host egg. Thus, the probability of detection decreases with clutch size.

Numbers of parasitic eggs actually discovered can then be corrected for a large part of their underestimation using the formula:

$$\text{Corrected number of parasitic eggs} = \frac{\text{Observed number}}{\sum P_i C_i}$$

where C_i is the proportion of all clutches of size i, and P_i is the probability of detection for that clutch size. Any parasitic eggs discovered outside the period considered for these calculations will not be underestimates, and should be added directly to the above result.

The probabilities of detection show large differences according to the assumptions of the calculation, and different assumptions may be necessary for different studies. For instance, opportunities for brood parasitism may not be randomly distributed during egg laying and might occur more often at specific times in the egg-laying period (Fetterolf and Blokpoel 1984). Parasitic females might wait until the host has begun her clutch before laying a parasitic egg. In these cases, the total number of days on which parasitic eggs can be laid must be reduced in the calculation of the probability of detection.

In addition, application of the resulting estimates of the frequency of brood parasitism relies on homogeneity of parasitic egg-laying throughout a nesting season, or throughout a nesting habitat. If the frequency of parasitism is known to vary with respect to some recognizable feature, a stratified estimate should be employed.

A potential shortcoming of our method is that we assume only one parasitic egg is laid in any clutch. If more than one is actually laid, our method gives a gross underestimate of the actual frequency of brood parasitism. Thus, this method is not accurate for use with species that are known to have multiple parasitic eggs in some nests.

It should be clear from this investigation that daily nest checks may underestimate the actual frequency of brood parasitism by a large fraction. The method presented here leads to a conservative, but much truer, estimate of the actual frequencies of brood parasitism.

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Recoveries of Sooty Terns (*Sterna fuscata*) on Saba Cay, St. Thomas, U.S. Virgin Islands.—Movements of terns within the Caribbean region are not well known (Halewyn and Norton 1984), yet recent reports of population mixing (Furniss 1983, Norton 1984, W. B. Robertson, pers. comm., Schaffner et al. 1986) document recruitment between colonies 35–1700 km apart.

Saba Cay is a 30 ha islet located 6 km WSW of Charlotte Amalie (Fig. 1). The south coast rises 60 m above the sea and on the north coast two brackish ponds occupy most of the lowlands. We estimated over 40,000 Sooty Terns (*Sterna fuscata*) nest on the slopes among cacti (*Cactus inornatus, Opuntia ripens*), shrubs (*Leucaena glauca, Clerodondron aculsatum*), *Ficus* sp., sedge (*Cyperus* sp.) and a thick growth of grass (*Panicum maximum*).

Between 1976 and 1985 teams of volunteers and staff from the Division of Fish and Wildlife visited Saba Cay to band Sooty Terns. We hoped by banding young and adults over a period of time to determine whether young we banded returned to Saba to breed, at what age they returned, and whether or not birds banded in other colonies were nesting at Saba. From 1976 to 1980 we visited Saba weekly or biweekly from late April to August, banding from 0800 to 1100 hr and from 1400 to 1600 hr. Banding groups included up to 20 people. We stopped banding during the middle of the day because the sun was too intense and we did not want to keep the birds off their nests during the hot period.

In May we concentrated on capturing adults on or near their nests by hand. Adults incubating in tall grass seemed reluctant to fly when approached slowly and could be caught on the nest, but we caught most of them as they left the nests. Almost all of the young hatched by the first week of June and from this date on we banded young almost exclusively. Young terns hid under vegetation. We searched likely areas and banded juveniles as we found them.

Between 1981 and 1985, although our methods were similar to those outlined above, we reduced the number of volunteers and staff to less than 5 on each visit to lessen colony disturbance. We visited the island once a week during May and June and weekly or biweekly in July.