

COMMENTARIES

Patterns of Egg-laying in Prairie Ducks

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Cole (1917) defined an indeterminate layer as one that both extends laying when eggs are removed and curtails laying when eggs are added to the nest. Rohwer (1984) experimentally showed that some captive, wild-stock Mallards (*Anas platyrhynchos*) extended laying when eggs were removed, but the same treatment did not induce extended laying in wild Mallards or wild Blue-winged Teal (*Anas discors*), in smaller samples of Gadwalls (*Anas strepera*), Northern Shovelers (*Anas clypeata*), or Canvasbacks (*Aythya valisineria*), or in a Green-winged Teal (*Anas crecca*). Nor did wild Blue-winged Teal curtail breeding when eggs were added to their nests. Rohwer (1984) removed and added eggs during the first part of the laying period in his experiments. The fourth and all subsequent eggs were removed from wild birds, the third and subsequent eggs were removed from captive birds, and 6 or 8 eggs were added to nests that already contained 2 or 3 eggs.

From these experiments, Rohwer (1984), (1) concluded that wild ducks do not lay indeterminately, as has been reported previously (Delacour 1964, Andersson and Eriksson 1982), and (2) suggested that nutrition is not the proximate determinant of clutch size in prairie ducks because eggs had to be removed for extended laying to occur. These conclusions may not be valid.

In a review of clutch-size determination in birds, Klomp (1970: 102) gave a critical test for distinguishing between direct and indirect proximate effects of food on clutch size of indeterminate layers. Indeterminate layers will not protract laying when eggs are removed from the nest if food has a direct proximate effect, but will if the effect of food is indirectly proximate. By extension, laying will not be curtailed when eggs are added if the effect of food is direct, but will be if it is indirect. Food has a direct proximate effect on clutch size if it influences the physical condition of the female, so that the number of eggs produced is determined by the amount of material available for yolk and albumin production. Food has an indirect proximate effect on clutch size if it influences the physiological mechanism controlling ovarian ac-

tivity. The critical point is that laying will not be extended or curtailed in indeterminate layers if food has a direct proximate effect on clutch size.

Whether food has either or both proximate and ultimate effects on clutch size is unclear. Rohwer (1984) suggested that food is not a proximate determinant. Bengston's (1971) data on diving ducks imply the reverse. Ankney and MacInnes (1978) suggested that clutch size in female Lesser Snow Geese (*Chen caerulescens caerulescens*) is determined by the size of her nutrient reserves, and hence that much variation in clutch size between females is caused by proximate rather than ultimate factors. Batt and Prince (1979) considered laying date to be the main factor controlling clutch size in Mallards and noted that the proximate effect of food may not be the only reason for variation in laying date. Their results indicated that food ultimately affects individual laying date, and hence clutch size. But they did not specifically reject a proximate influence of food on clutch size.

Rohwer's (1984) data on clutch manipulation in wild ducks are consistent with a direct proximate effect of food on clutch size of an indeterminate layer. His data from some captive ducks are consistent with an indirect proximate effect of food on clutch size of an indeterminate layer. None of his data refute the possibility that ducks are indeterminate layers or that their clutch size is influenced proximately by food. I suggest that the question of whether wild ducks are determinate or indeterminate layers remains unresolved. Further experimental studies appear warranted.

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Counting Seabirds at Sea from Ships: Comments on Interstudy Comparisons and Methodological Standardization

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In a recent paper Tasker et al. (1984) addressed the difficulties of counting seabirds at sea. They reviewed quantitative seabird surveys and discussed the various methodologies these surveys used. Their treatments of the biases inherent in detecting seabirds and the implications of these biases to survey methods are comprehensive and significant to anyone concerned with improving seabird research design. These authors concluded by advocating the use of a standardized sampling method (300-m band transect) that would allow comparisons between studies and distinguish between sitting and flying bird densities to reduce bias of flying birds when estimating density. The authors' criticism of various other methods was that they "cannot provide data for the calculation of absolute abundances." They maintained that this precludes comparisons, apparently based on abundance, between different studies.

I have surveyed seabirds in the South Atlantic Bight off the southeastern United States for two and one-half years using a band-transect method very similar to that used by Tasker and colleagues. My experiences have led me to question whether calculations of absolute abundances are possible without considerable additional qualifications. I discuss these qualifications, elaborate on the problems of counting flying birds during seabird censusing, and question the present implementation of standardized seabird survey methods. I should relate that my study of a subtropical and tropical seabird fauna, primarily from an oceanographic perspective, interjects a certain regional and disciplinary "bias." Ecological patterns of seabird faunas and species in tropical marine environments may be quite different from the high-latitude, temperate-boreal communities (e.g. alcid, penguins, etc.) that Tasker et al. cite in their treatment.

One of the major recommendations by Tasker et al. was to correct for the movement of flying birds in the band transect by using separate instantaneous

counts within each counting block. Instantaneous counts of flying birds in the whole block are "impossible" due to observer inability to detect all birds at distances exceeding much more than 200-300 m. They correctly noted that counts of all seabirds seen to pass through the zone covered by the band transect would overestimate bird density and actually would be a measure of "flux" (see also Wiens et al. 1978).

Tasker et al. (1984: 572) suggested that a distinction (for comparative purposes) be made between sitting and flying bird densities as a means to compensate for overestimation of bird density caused by flux. Such a distinction is difficult for some species (e.g. feeding storm-petrels), and in some studies it may create as many problems as it attempts to solve. Seabirds sitting on the ocean surface are not necessarily more interactive with their environment. Seabird faunas in some regions may be totally or nearly lacking in species that spend any appreciable time on the ocean surface. For example, after two years of seabird counts in Gulf Stream waters on the Blake Plateau off the southeastern United States, I found that Black-capped Petrels (*Pterodroma hasitata*) and Sooty Terns (*Sterna fuscata*) were numerically dominant. Both species forage and feed on the wing. The former species was rarely and latter species never observed on the water surface. This type of ecological variation between regions would seriously complicate between-study comparisons based on absolute abundances separated into flying and sitting bird densities.

Because seabirds are not sessile marine organisms and do not permanently occupy any unit of ocean surface area at the time and space scales sampling usually is undertaken, absolute abundances are difficult, if not impossible, to obtain. The residence times of sitting birds that are feeding or resting on a given patch of ocean might be longer than that of flying birds. Eventually, however, sitting birds will move into another, adjacent patch of ocean in the same manner that flying birds do. Theoretically, the residence times of sitting and flying birds generally increase with increasing patch size until some upper

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