

this species as *Spreo torquata*, but for the present its relationships remain obscure.

A systematic revision of the African starlings is long overdue. Our results suggest that the composition of the genera *Cinnyricinclus*, *Cosmopsarus*, *Lamprotornis*, and *Spreo* should be reexamined.

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Clutch Size, Daylength, and Seasonality of Resources: Comments on Ashmole's Hypothesis

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Clutch size tends to increase with latitude both within and among bird species. For nidicolous birds, Lack (1947) suggested this might be due to the longer daylength at higher latitudes that allowed parents to collect more food and feed larger broods. Ashmole (1961) proposed an alternative hypothesis: that clutch size depends on the relationship between resource level and population density during the breeding season. If populations are limited by nonbreeding season resources, clutch size will increase as the seasonality of resources increases, regardless of average resource level. Ricklefs (1980) called this Ashmole's hypothesis. I am prompted by the recent renewal of interest in this topic (Ricklefs 1980; Koenig 1984a, b; Møller 1984) to offer some comments on the mathe-

matical representation and predictions of Ashmole's hypothesis.

Ricklefs (1980) introduced the notion that fluctuation in food resources available to bird populations can be represented by the seasonal pattern of actual evapotranspiration (AE). He expressed Ashmole's hypothesis in terms of summer and winter AE as

$$\text{clutch size } (C) = aS/W, \quad (1)$$

where a is an arbitrary constant, S is summer (breeding season) AE, and W is winter (nonbreeding season) AE. In this formulation, clutch size is directly proportional to seasonality of resources (i.e. the ratio of summer to winter AE) and does not depend on the absolute level of resources.

TABLE 1. Spearman rank correlation coefficients (r_s) for relationships among clutch size and several other variables.^a

	Clutch size	Latitude	Breeding season	W	S	S - W
Clutch size	—	0.69**	-0.68**	-0.68**	-0.37	0.53*
Latitude	13	—	-0.68**	-0.93**	-0.67**	0.62*
Breeding season	11	11	—	0.85**	0.70*	-0.52
W	12	12	10	—	0.73**	-0.58*
S	12	12	10	12	—	0.08
S - W	12	12	10	12	12	—

^a Data from Ricklefs (1980: Table 1). r_s is given above the diagonal (* = $P < 0.05$, ** = $P < 0.01$) and sample size below the diagonal. Calculations performed by SPSS program NONPAR CORR (Nie et al. 1975). The r_s value of -0.45 ($P > 0.05$) given by Ricklefs (1980: 44) for the correlation between clutch size and W is incorrect (Ricklefs pers. comm.).

As Ricklefs (1980) correctly depicted in his Fig. 1, however, and noted in the caption thereto, under Ashmole's hypothesis "clutch size is proportional to the ratio of the breeding season surplus to the adult population" (italics added). Or, more precisely stated, clutch size is proportional to the ratio of surplus breeding season resources (i.e. surplus to those needed to maintain the adult population) to winter resources. Because winter resources are postulated to limit population size, the winter resource level equals the portion of summer resources required to maintain the adult population in summer. The remaining summer surplus is available to the population for reproduction. Thus, instead of Eq. (1), Ashmole's hypothesis should be expressed as

$$C = a(S - W)/W, \quad (2)$$

where a is a new constant and S and W are as previously defined. Equation (2) provides for use of a portion of summer resources to maintain the adult breeding population, whereas Eq. (1) devotes summer resources entirely to reproduction.

In a completely seasonless environment, $S = W$ and Eq. (2) gives $C = 0$. This is correct under a strict interpretation of Ashmole's hypothesis since breeding would not occur if there were no surplus resources. As Ashmole (1961) suggested, however, under such extreme conditions in the real world we would expect breeding to occur at all times of the year and clutch size to be low. Surplus resources would be scarce and would be created by temporary reductions of the population below the level that could be maintained by the resource base. Obviously, such refinements are not represented by Eq. (2), which models only the major features of Ashmole's hypothesis. Moreover, the relationship between clutch size and AE operates through the food supply and is likely to be more complex than the direct proportionality of the equation.

Ricklefs (1980) determined that there was a significant correlation between C and S/W (Spearman rank correlation, $r_s = 0.65$, $P < 0.05$, for 12 localities). He

also performed a multiple regression-partial correlation analysis of the same data, using the generalized transformed form of Eq. (1):

$$\log C = \log a + b \log S - c \log W, \quad (3)$$

which showed that clutch size was inversely correlated with winter resources but was not correlated with summer resources. Koenig (1984b) used the same procedure for the Northern Flicker (*Colaptes auratus*), with similar results. The equivalent generalized transformation of Eq. (2) is

$$\log C = \log a + b \log(S - W) - c \log W, \quad (4)$$

and the corresponding analysis distinguishes between the effects of summer surplus ($S - W$) and winter resources (W) instead of between summer and winter resources.

Application of this analysis to Ricklefs's (1980) data shows that $\log W$ remains significantly inversely correlated with $\log C$ but that $\log(S - W)$ is not correlated with $\log C$ after controlling for $\log W$ (Ricklefs pers. comm.). However, the ability to distinguish between the effects of $\log(S - W)$ and $\log W$ in this analysis is relatively poor since these two variables are significantly correlated with each other ($r = -0.65$, $P < 0.05$) whereas $\log S$ and $\log W$ are not significantly related ($r = 0.32$, $P > 0.05$).

Following Ricklefs (1980), Møller (1984) suggested several predictions from Ashmole's hypothesis: (1) clutch size and level of winter resources should be negatively correlated, (2) clutch size and level of summer resources per breeding pair should be positively correlated, (3) clutch size and the relation between summer and winter resources should be positively correlated, and (4) clutch size and summer resource level should vary independently. Møller's predictions (1) and (4) do not follow directly from Ashmole's hypothesis, however, but derive from the subsidiary hypothesis that winter resource levels (or breeding densities of adults) are primarily responsible for the correlation, if any, between C and S/W , as found by Ricklefs (1980). Møller's prediction (3)

follows from Eq. (1) if we read "ratio of summer to winter resources" for "relation between summer and winter resources," and it remains correct under Eq. (2).

If Ashmole's hypothesis is true, we would expect clutch size and resource data to be consistent with its predictions. We must not be seduced by an attractive hypothesis, however, into believing that correlation of climatic or other environmental variables with clutch size provides more than meager support for any hypothesis. Many, perhaps most, environmental and biological variables are correlated with latitude and also will be correlated with clutch size in those avian species and groups within which clutch size varies with latitude. It is not surprising, therefore, to find that clutch size is often positively correlated with daylength (e.g. Hussell 1972) and is negatively correlated with winter AE (Ricklefs 1980; Koenig 1984a, b). The data in Ricklefs (1980: Table 1) show that clutch size is correlated with winter AE, latitude (and therefore maximum daylength), length of breeding season, and summer AE minus winter AE (Table 1). Moreover, most pairs among these variables are significantly related (Table 1). Koenig (1984b) shows that neither winter AE nor breeding density accounts completely for the latitudinal trend in his clutch size data. Clearly, the possibility remains that the latitudinal trend in clutch size may be explicable in terms of any of these variables or a complex relationship among several of them or others not considered here (e.g. see Royama 1969). Demonstration of a correlation between clutch size and an environmental variable provides little insight into the causative agents of clutch size determination and merely allows that variable to remain as a viable candidate for consideration as an element of an explanatory hypothesis. We need to find other ways to test such hypotheses.

Finally, in his discussion of Ashmole's hypothesis, Lack (1968: 167) noted that "while the summer day is about one-and-a-half times as long in mid-Europe as in the tropics, the average passerine clutch is twice as large, so some factor in addition to daylength must be concerned." Although Lack attributed this insight to Ashmole, apparently it was not his (Ashmole 1961 and pers. comm.). It is not necessary to invoke factors other than daylength available for feeding young to explain the observed differences in clutch size between the tropics and mid-Europe (Hussell 1972). As with food resources, it is the surplus available for reproduction that is important in the postulated relationship between daylength and clutch size. Consider a hypothetical example: If daylength is 12 h in the tropics and 18 h in mid-Europe (i.e. 1.5 times greater), and if adults spend 6 h feeding and maintaining themselves at each locality and devote the remainder of the day (6 h in the tropics and 12 h in

Europe) to raising their broods, then the observed clutch size ratio of 2 between Europe and the tropics is exactly as expected from the daylength hypothesis alone. Although it is unlikely that adult birds use exactly the same amount of time to maintain themselves in the Temperate Zone as in the tropics, this example shows that time budgets of the adults influence the extent to which the discrepancy between the clutch size and daylength ratios is unexplained by the daylength hypothesis. Very little is known about variation in time budgets of birds breeding at different latitudes, and more detailed examination of this aspect of the problem may prove to be fruitful. Nevertheless, more than correlational evidence will be necessary to determine whether daylength, seasonality of resources, other variables, or several variables acting together are primarily responsible for the evolution of geographic variation in clutch size.

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