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Allocation of Limited Reserves to a Clutch: A Model Explaining the Lack of a Relationship Between Clutch Size and Egg Size

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Lack (1967, 1968) proposed that clutch size in waterfowl is limited by the nutrients available to females when producing eggs. He suggested that if nutrients available for clutch formation are limited, then species producing small eggs would, on average, lay more eggs than species with large eggs. Rohwer (1988) argued that this model also should apply within species. Thus, the nutrient-limitation hypothesis predicts a tradeoff among females between clutch size and egg size (Rohwer 1988). Field studies of single species consistently have failed to detect a negative relationship between clutch size and egg size (Rohwer 1988, Lessells et al. 1989, Rohwer and Eisenhauer 1989, Flint and Sedinger 1992, Flint and Grand 1996). The absence of such a relationship within species has been regarded as evidence against the hypothesis that nutrient availability limits clutch size (Rohwer 1988, 1991, 1992; Rohwer and Eisenhauer 1989).

Failure to detect a negative correlation between clutch size and egg size is not necessarily evidence against regulation of clutch size by nutrient reserves. If both clutch size and egg size are correlated with a third variable, then variation in the third variable could conceal a correlation between clutch size and egg size at the population level. In this paper we discuss evidence that both nutrient reserves and egg size are positively correlated with body size for species that rely on reserves for egg production, and we explore how these correlations might influence detection of tradeoffs between clutch size and egg size.

We have assumed that individual females have a fixed amount of reserves available for the entire reproductive attempt (i.e. clutch formation and incubation) and a phenotypically fixed egg size. Waterfowl, in general, show high repeatability of egg size, suggesting that females cannot (or do not) alter their egg size in response to nutrient reserves or environmental conditions (e.g. Flint and Grand 1996). Reserves are used for egg production, but optimal investment in the clutch is less than the maximum possible (Fig. 1) because reserves are retained for use during incubation (Klomp 1970, Ryder 1970, Raveling 1979, Ankney 1984, Ankney and Alisauskas 1991, Gloutney and Clark 1991, Afton and Paulus 1992, Erikstad et al. 1993, Mann and Sedinger 1993). Under this model, females can trade investment in the clutch for reserves retained for incubation (Erikstad et al. 1993). That is, to complete the last laid egg in a clutch (i.e. the unshaded egg in Fig. 1), a female may use reserves that ideally would be saved for incubation. Females that begin incubation with smaller reserves than optimal may compensate by taking more or longer incubation breaks (i.e. the "risky" strategy of Ankney and Alisauskas [1991]).

Using simulated data, we used two variations of the basic concept outlined above: (1) the "Random Model," in which no correlation exists between reserves and egg size; and (2) the "Correlation Model," in which reserves are positively correlated with egg size. In the random model, we assumed that reserves used for egg production are randomly distributed among females with different egg-size phenotypes. We used this simple approach to confirm that a negative relationship between clutch size and egg size could reasonably be expected under the nutrient-limitation hypothesis. The correlation model is based on studies that show a positive relationship between body size and egg size for a range of waterfowl species (Newell 1988, Rohwer 1988, Larsson and Forslund 1992, Flint and Grand 1996, Sedinger unpubl. data; but see Cooke et al. 1995). Additionally, Duncan (1987) found a positive relationship between body mass during incubation and egg size for Northern Pintails (*Anas acuta*). Furthermore, studies of Lesser Snow Geese (*Chen caerulescens caerulescens*) suggest that larger-bodied females have the potential to store more nutrient reserves before egg laying (Ankney and MacInnes 1978, Alisauskas 1988, Alisauskas and Ankney 1990). Sedinger et al. (1995) showed that large-bodied Black Brant (*Branta bernicla nigricans*) laid clutches of greater total volume than did smaller females, and they concluded that this result was consistent with the model that larger-bodied females stored more reserves. Finally, Alisauskas et al. (1990) showed that body size was positively related to nutrient reserves before egg laying in Ring-necked Ducks (*Aythya collaris*).

The combination of these positive relationships between (1) body size and egg size, and (2) body size and reserves creates the potential for a positive correlation between egg size and the amount of reserves available for egg production. In fact, Hepp et al. (1987)

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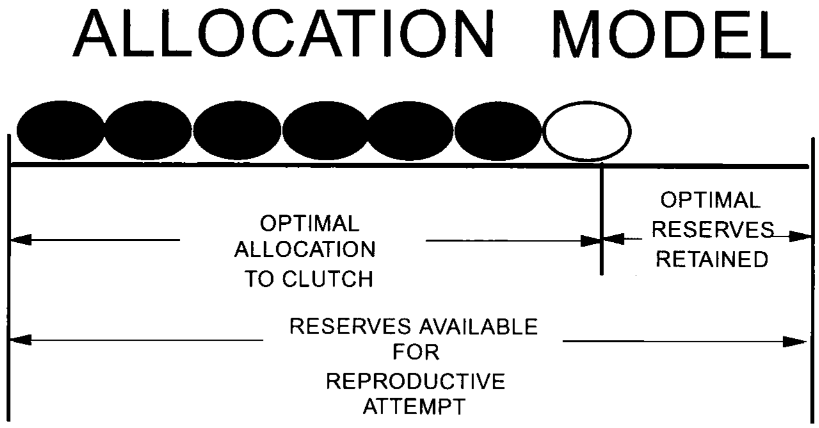

FIG. 1. Model of allocation of limited reserves to a clutch of eggs. This model allows females to trade investment in the clutch for reserves retained for the remainder of the reproductive attempt. In this example, production of the final egg (i.e. unshaded) used a small portion of the reserves normally retained for incubation.

found a positive relationship between prelaying reserves and egg size and a positive but nonsignificant relationship between body condition and clutch size in Wood Ducks (*Aix sponsa*). Thus, among waterfowl that rely on endogenous reserves for egg production, large-bodied birds may tend to lay larger clutches of larger eggs than do small-bodied birds. This positive correlation between clutch size and egg size could disguise the tradeoff between clutch size and egg size that might exist among females.

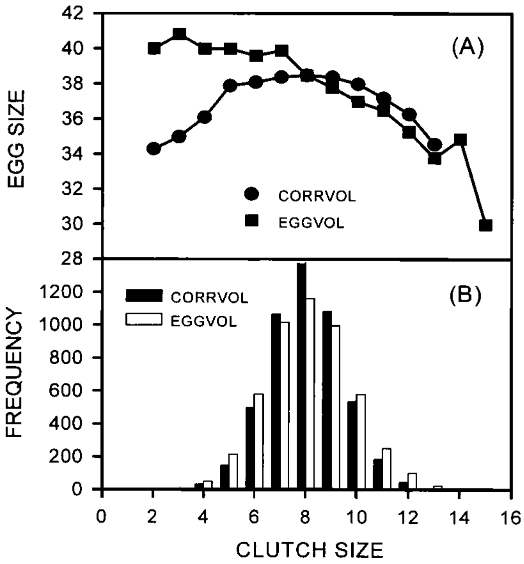

FIG. 2. (A) Relationships between clutch size and EGGVOL (i.e. egg size from random model) and clutch size and CORRVOL (i.e. egg size from correlation model). (B) Frequency distributions of predicted clutch sizes from the two models.

Methods.—We generated simulated data sets assigning 5,000 females a random quantity of reserves to allocate to egg production (RESERVES; i.e. optimal investment from Fig. 1) and a random egg size (EGGVOL), based on means and standard errors for total clutch volume and egg size for Northern Pintails from Flint and Grand (1996). We then assigned individual females a second egg volume (CORRVOL) that was correlated with RESERVES using the following equation:

$$\mathrm{CORRVOL}_i = (32.64 + \pi_i) + (\mathrm{SLOPE} + \xi_i) \cdot \mathrm{RESERVES}_i, \qquad (1)$$

where SLOPE is the relationship between RESERVES and CORRVOL. Thus, for female i, π_i and ξ_i are random normal deviations from the Y-intercept and slope. For a given slope we adjusted the variance parameters (π_i and ξ_i) until the standard deviations of EGGVOL and CORRVOL were equal. We determined clutch size by dividing RESERVES by EGGVOL and CORRVOL and rounding to the nearest integer. Mean EGGVOL and CORRVOL were calculated within each predicted clutch size for both models.

We examined the effect of the strength of the relationship between CORRVOL and RESERVES on our ability to detect a tradeoff between clutch size and egg size. We initially allowed CORRVOL to increase 0.005 ml per ml of RESERVES (i.e. slope) for the correlation model and then we increased the slope in units of 0.005 until we failed to detect a negative relationship between clutch size and CORRVOL. Thus, we attempted to determine the slope required to override detection of a clutch size-egg size tradeoff.

Results and Discussion.—EGGVOL declined with clutch size. CORRVOL, however, peaked at a clutch of eight eggs (Fig. 2A), and the relationship with clutch size was relatively flat over the common clutch sizes (Fig. 2B) when we used a slope of 0.019 ($r^2 = 0.14$) between CORRVOL and RESERVES. Therefore, a weak correlation between reserves available for clutch formation and egg size eliminated a clutch size-egg size tradeoff in our simulated data. To the extent that a positive relationship between reserves and egg size exists in natural populations, the correlation model described here explains the failure of field studies to detect a negative relationship between clutch size and egg size.

The predicted mean EGGVOL declined with clutch size as expected. The random model thus demonstrates why researchers have suggested that a negative relationship between clutch size and egg size is a logical outcome of the nutrient-limitation hypothesis. The slope of this relationship, however, was only slightly negative (i.e. only 3 cm^3 difference in EGGVOL expected between clutches of 5 and 10 eggs). Inclusion of a correlation between egg size and nutrient reserves removed this negative trend. Therefore, we interpret the relationship between EGGVOL and clutch size (Fig. 2) as predicting the steepest possible slope to be expected in the absence of a correlation between egg size and nutrient reserves. Thus, it is possible that egg size is randomly distributed with respect to reserves and that the failure of field studies to detect a negative relationship between clutch size and egg size is due to insufficient statistical power. We encourage researchers examining clutch size-egg size tradeoffs to conduct a modeling exercise similar to the one presented here (using appropriate egg size and optimal reserves numbers for their study species) and to determine the power of their analysis based on field data to detect the slope predicted from the model.

The predicted mean CORRVOLs are not linearly distributed with respect to clutch size. The largest eggs occur in the most common clutch sizes (Figs. 2A and 2B). This is not the result we expected. We believe this result occurs because small egg sizes in small clutches are driven by the positive relationship between egg size and nutrient reserves, whereas small egg sizes in large clutches result from clutch size-egg size tradeoffs. The correlation model predicts essentially no relationship between clutch size and egg size over the normal range of clutch sizes (i.e. 4-11 eggs). We are aware of no data that would allow a direct test of this hypothesis. Until alternative models of nutrient allocation have been tested, it is inappropriate to reject the nutrient-limitation hypothesis due to failure to detect a clutch size-egg size tradeoff within species.

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Notes on the Behavior of the Masked Saltator in Southern Ecuador

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The Masked Saltator (*Saltator cinctus*) is a near-threatened species (Collar et al. 1994) that is locally distributed in Andean cloud forest from central Colombia to central Peru (Renjifo 1991). Contrary to assumptions that it is a shy inhabitant of impenetrable undergrowth (O'Neill and Schulenberg 1979, Ridgely and Tudor 1989), it has been recorded in Colombia joining large mixed-species flocks in the canopy (Renjifo 1991). Additionally, its association with *Chusquea* bamboo in Peru (O'Neill and Schulenberg 1979) is not apparent in Colombia (Renjifo 1991). We confirm Renjifo's findings in a population of *S. cinctus* in Ecuador, and present data suggesting that the species, unlike most cloud-forest passerines, undertakes nonseasonal movements. This behavior possibly derives from a dependence on the cone crop of podocarps (Podocarpaceae).

On two separate visits in 1990 and 1991, we surveyed birds on the Cordillera de Sabanilla, above the town of Amaluza, Loja Province, southern Ecuador (4°21'S, 79°45'W). Our main site was Angashcola, a valley on the western slope of the main Andean cordillera that retained ca. 300 ha of montane cloud forest contiguous to large areas of similar vegetation in adjacent valleys (Williams and Tobias 1994). This habitat extended northward to the extensive forests within Podocarpus National Park and southward into Peru. Podocarps, primarily *Podocarpus oleifolius*, were exceptionally common in the area. All forest below 2,450 m had been removed, and the upper tree line extended little beyond 3,000 m because of clearance at the páramo edge (Williams and Tobias 1994). Meteorological conditions were very similar during both of our visits.

From 1 to 17 August 1990, *S. cinctus* was seen almost daily at Angashcola (21 sightings of 1 to 3 birds together; 33 individuals total). Although the species often was conspicuous and confiding, it was only located at the lower fringe of forest, between 2,450 and 2,550 m. It also was never recorded in bamboo despite our spending ca. 90 h surveying this habitat and an additional 35 h running 24 m of mist nets where

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