Variance in clutch size

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Summary. Most studies of the evolution of clutch size have concentrated on changes in the mean and have neglected the variance of clutch size. We suggest that the variance is very important and discuss how it might be fruitfully analyzed.

In developing his theory of the determination of clutch size by natural selection, Lack[2] proposed that the mean clutch size observed for any given species in any given environment corresponded to the largest mean number of young for which the parents could provide food. While this theory has been strongly criticized, and to some extent modified, it is now generally accepted (see Owen[3] for a review).

However, it is notable that with few exceptions variance in clutch size is rarely discussed or treated in considering this important evolutionary problem[4]. For example, Charnov and Krebs[5] noted specifically that 'Lack's hypothesis made no prediction about variations round the most productive clutch', but did not incorporate variance into their theory of optimal clutch size, defined as that which maximizes an individual's fitness.

Similarly, very few investigations of the inheritance of clutch size have been conducted, though this is obviously of considerable importance in assessing the theory. However, a bird with very variable clutch size,[6] the great tit, had a narrow sense heritability of clutch size of approximately 0.5. It would be of great interest to have similar values for birds with highly invariant clutch size, but in such cases very large numbers of data would be needed.

Gillespie[7] has considered a model for the genetic determination of both location and dispersion of clutch size, which in fact allows only very tightly constrained fecundity distributions to be stable[8]. This appears to be because increasing the variance in offspring number of a genotype decreases its fitness[8,9].

The model of greatest interest is that of Heyde[10,11]. Unlike Gillespie, Heyde has used an infinite population size model, but he has shown that maximization of the probability of survival of the species to time, t, can occur through the evolution of a characteristic clutch size fixed at either a single value, k, or a pair of values, k, k+1. Heyde's model requires that there be a constant 'maximum number of young which the parents can raise on the average'. Now if there is any variation about this mean, it follows that in some generations more young than this mean number must be raised. Accordingly, it must be some other property of clutch size, such as the actual physical or physiological upper limit on the number of eggs which can be laid, which is the ultimate determinant of clutch size distribution. A preliminary investigation of this problem should begin by attempting to loosen the restriction that the maximum mean number of rearable offspring be constant over a period of time.

None of the models discussed above covers the case of the shore birds shown in table 1. The simplest description of these distributions is to say they are canalized, in Waddington's[12] sense, though not necessarily at the same value (cf. *Charadrius alexandrinus* in Australia and North America). The question of interest is what kind of process yields these triangular or binomial distributions? McLean[13] has suggested that 4 was the ancestral clutch size of the Charadrii, as no member species 'normally lays a clutch of more than 4, regardless of its degree of specialization'. It is not clear (cf. table 1) that this is completely correct; evidently canalization to the modal number is less rigid than, say, in albatrosses[14]. However, if we ignore the small members of clutches larger than the modal size, we may regard deviations downwards within a species as the raw material on which natural selection has acted in speciation.

Treating clutch sizes of 4, 3, 2 and 1 as deviations from the mode of 0, 1, 2 or 3, we may examine the fit to one process which might describe, if not explain, the variation. This is the 'burnt fingers' process, a name applied by Arbous and Kerrich[15] to the case of accidents in industry, where, until an accident occurs, an individual has a given, constant chance of having an accident, and, when this happens,

Table 1. Clutch sizes recorded in RAOU and NANRS records

	Species	Clutch size					
		1	2	3	4	5	6
Australia	Banded plover *Vanellus tricolor (Zonifer tricolor)*	5	5	27	86	0	0
	Spur-winged plover *Lobibyx novae-hollandia*	21	47	117	300	2	1
	Red-capped dotterel *Charadrius alexandrinus*	26	168	3	0	0	0
	Black-fronted dotterel *Charadrius melanops*	8	38	62	1	0	0
USA	Snowy plover *Charadrius alexandrinus*	3	5	11	1	0	0
	Piping plover *Charadrius melodus*	1	4	7	30	0	0
	Wilson's plover *Charadrius wilsonia*	6	4	19	0	0	0
Scotland	Dotterel *Eudromias morinellus*	2	33	376	1	0	0

Clutch size shown is maximum recorded where first observation relates to a nest containing at least one egg and no young. Dotterel clutch size distribution from Nethersole-Thompson[18].

Table 2. Estimates of the parameters of the 'burnt fingers' distribution

Species	$\hat{\delta}$	$\hat{\varepsilon}$	Goodness of fit
Banded plover	0.357	0.765	$\chi_1^2 \simeq 5.28$*$0.05 > P > 0.02$
Spur-winged plover	0.480	0.891	$\chi_1^2 \simeq 0.69$ $0.5 > P > 0.3$
Piping plover	0.336	0.947	$\chi_1^2 \simeq 0.27$*$0.7 > P > 0.5$

* Based on expectations at least one of which was less than 5.

immediately 'learns' enough to lower his chance of having further accidents. This crude model allowed the development of a satisfactory distribution where, in time (0,t), the probability of an accident occurring is δ, but thereafter falls to ε, i.e. $1 > \delta > \varepsilon > 0$.

The probabilities of 0, 1, 2 ... accidents in time intervals of length t are:

$$p(0) = e^{-\delta t}$$

$$p(1) = e^{-\varepsilon t} \frac{\delta}{\varepsilon - \delta} [e^{(\varepsilon - \delta)} - 1]$$

$$p(2) = e^{-\varepsilon t} \frac{\delta \varepsilon}{(\varepsilon - \delta)^2} [e^{(\varepsilon - \delta)t} - 1 - (\varepsilon - \delta)t]$$

$$p(3) = e^{-\varepsilon t} \frac{\delta \varepsilon^2}{(\varepsilon - \delta)^3} \left[e^{(\varepsilon - \delta)t} - 1 - (\varepsilon - \delta)t - \frac{(\varepsilon - \delta)^2 t^2}{2!} \right]$$

The parameters δ and ε may then be estimated, and this has been done for the clutch size of the banded plover, spur-winged plover and piping plover, with the results shown in table 2. Since $\varepsilon > \delta$, these results are not in agreement with the model. (This arises because the mean clutch size $\bar{x} > \delta$). An implication of the model might be that if the clutch sizes of particular species were simply the result of random fixation of genetic variation lowering clutch size, the distribution of modal clutch size among species would also be approximately triangular. Table 3, condensed from table 1 of McLean[13], shows that this is not the case.

Table 3. Mode or range of clutch size of 319 species of Charadrii[13]

Modal clutch size	Number of species
4–6	1
4–5	1
4	137
3–5	3
3–4	16
3	25
2–4	19
2–3	32
2	64
1–4	3
1–3	4
1–2	9
1	5

Little, if anything, is known of the relationship of the cost of reproduction to variability in reproductive performance, yet this cost is critical[16,17]. An analysis of variability in terms of this cost, possibly using developments of Heyde's methods, is vitally necessary.

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Multiple phosphoglucomutase alleles in *Toxorhynchites splendens* (Diptera: Culcidae)[1]

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Summary. Multiple phosphoglucomutase (E.C. 2.7.5.1) alleles are found in the mosquito *Toxorhynchites splendens.* The sample studied reveals 3 *Pgm* alleles whose frequencies are in good accord with Hardy-Weinberg expectations. The most frequent allele is that controlling a phenotype with an intermediate electrophoretic mobility. Each *Pgm* allele determines a two-band electrophoretic pattern.

Electrophoretic data on gene-enzyme systems in mosquitoes reveal very frequent occurrence of multiple alleles. Of these, phosphoglucomutase (E.C. 2.7.5.1) and esterase (E.C. 3.1.1.1) are the most extensively studied[2,3]. Although many mosquito species have been studied, they belong mainly to 3 genera, *Anopheles, Aedes* and *Culex.* There appears to be no previous report on the genus *Toxorhynchites* Theobald. Members of this genus are large, non-biting mosquitoes. We report here the presence of multiple phosphoglucomutase alleles in *Toxorhynchites splendens.* This and other species of *Toxorhynchites* are considered beneficial to man because a) their larvae are predaceous on other mosquito larvae, and b) the adults may be used for rapid isolation of Dengue-fever virus[4].