Spacing Behavior and Population Limitation in Red Grouse

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In their commentary on Blue Grouse (*Dendragapus obscurus*), Bergerud and Butler (1987) misrepresented our work on Red Grouse (*Lagopus lagopus scoticus*), so we reply briefly here. Earlier, we (Watson and Moss 1987) criticized the position taken by Bergerud et al. (1985) and now repeated by Bergerud and Butler, and every aspect of our critique remains valid despite Bergerud's (1987) response.

Bergerud and co-authors contend that two hypotheses to explain changes between years in the spring numbers of grouse are (1) the territorial self-regulation hypothesis and (2) the breeding-success hypothesis, that spring numbers change in response to variations in breeding success. The main evidence presented for hypothesis (2) was the occurrence of high correlation coefficients between breeding success and spring numbers. Bergerud et al. (1985) admitted that this was not a mutually exclusive test between the two hypotheses. Yet they went on to use such correlations, as did Bergerud and Butler (1987), as if their occurrence were mutually exclusive.

Referring to our model (Watson et al. 1984) that predicted change in spring numbers from prior breeding success, Bergerud and Butler (1987) stated that this was a *"de facto* rejection" of our territorial-spacing model. It is not. The main demographic cause of change in spring numbers was winter loss; breeding success was a useful predictor of change in spring numbers only because it happened to be correlated with subsequent winter loss (Watson et al. 1984). Bergerud and Butler (1987) stated that Watson and Moss "apparently now accept the breeding-success hypothesis" and "fail to acknowledge that it was proposed independently for cyclic *Lagopus* populations by Bergerud (1970)." Yet we (Watson and Moss 1987) made it clear that we do not accept the breeding-success hypothesis as a sufficient explanation of change in spring numbers. Also, long before Bergerud (1970), a relationship between spring numbers and prior breeding success was noted in Red Grouse (Jenkins et al. 1963, 1967) and Rock Ptarmigan (*L. mutus*; Watson 1965). Our hypothesis of territorial behavior limiting spring numbers has always incorporated the breeding-success correlation.

In a response to Watson and Moss (1987), Bergerud (1987) wrote "they should state what they will accept as a valid disproof of their territorial model," yet we had just stated this explicitly (p. 1045). In addition, a lack of the breeding-success correlation is a rejection of the breeding-success hypothesis. Although strong correlations between breeding success and change in

spring numbers are frequent in *L. lagopus* and Rock Ptarmigan populations, they do not always occur (Watson and Moss 1987).

Bergerud et al. (1985) applied their breeding-success hypothesis solely to *L. lagopus* and *L. mutus* but Bergerud and Butler (1987) now extend it to Blue Grouse and to grouse generally (their first sentence). Such correlations are weak or absent in most studies of grouse species other than *L. lagopus* and *L. mutus* (Moss 1987). Also, Bergerud and co-authors should recognize that high correlation coefficients can occur along with low regression coefficients. Hence, even if such a correlation is consistent, it can be demographically unimportant.

Bergerud and Butler (1987) stated that one reason the territorial hypothesis has lingered is that researchers have studied "inappropriate populations living in optimum habitats where ingress and egress confounded results." Population dynamics in optimal and other habitats may differ (Moss et al. 1982: 32), and mainland populations may differ from island ones (Watson and Moss 1979: 95–96). Mainland populations in optimal habitats may comprise most individuals in a species, however, and so are certainly not "inappropriate" for study. Moreover, it is odd that the normal, crucially important movement of animals into and out of populations should be thought to have "confounded" results. A major trend in modern population ecology is an increasing appreciation of the importance of movement to animal populations.

The evidence adduced by Bergerud and Butler (1987) for the breeding-success hypothesis rests on correlation coefficients, even though Bergerud et al. (1985) admitted that such correlations were not a mutually exclusive test between the two hypotheses. It is dangerous to confuse correlation with cause and effect. These are best distinguished by experiment.

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Growth-curve Analysis: A Critical Reevaluation

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Growth-curve analysis (Ricklefs 1967) has long en-
joyed an ardent following. Recently, Brisbin et al.
(1987) predicted a bright future for this methodology,
but failed to address critical shortcomings of growth-
curve analysis and of the Richards (1959) model in
particular. They also completely ignored alternatives.
Growth-curve analysis is a tool only, and not an end
in itself. The main question is not which model to
use, but whether to use growth-curve analysis at all.
For many studies growth-curve analysis is inappro-
priate, and alternatives, such as simple observed-
growth statistics, may be more effective growth
indicators. Although the Richards model with its vari-
able sigmoid shape is intuitively attractive, other sim-
pler models can be superior for studying growth.

There are many reasons growth-curve analysis may
not be an ideal methodology. Growth-curve analysis
is labor intensive because numerous data are required
to satisfy models with several fitted parameters. For
passerines, with their short nestling time, this usually
means daily measurement on a rigid schedule so that
each nestling is always measured at about the same
time. Alternatively, variable time must be taken into
account during curve fitting. Growth-curve analysis
requires numerous precise data. Small changes in only
a single measurement can profoundly affect param-
eter estimates. Sensitivity depends on the type of
model employed, however.

High data requirements of growth-curve analysis
can stress both parents and nestlings. Frequent dis-
turbances can cause nest abandonment and conse-
quent loss of data. During cold, wet weather it is often
difficult to keep small nestlings warm and dry; hence,
handling alone can significantly affect growth (Zach

and Mayoh 1986a). Subtle stress from disturbances
and handling is difficult to detect and confounds in-
terpretation of treatment effects.

A consistent finding is large variation in growth
among broods, commonly exceeding 50% of the total
variation (Ricklefs and Peters 1979, Zach and Mayoh
1982). Consequently, statistical power to test for treat-
ment effects is low unless a large number of broods
is studied. Unfortunately, growth-curve analysis re-
quires much effort per brood, making it difficult to
study many broods simultaneously.

For many passerines, growth-curve analysis is dif-
ficult to apply because fledging occurs well in ad-
vance of growth completion. Meaningful fitting of
growth curves requires precise estimates of final size.
Body-mass recession may also occur before fledging
(Ricklefs 1968a). There seems to be little agreement
on how to deal with this phenomenon. We have used
data up to, and including, the highest body mass be-
fore fledging, but this may not be entirely appropri-
ate. Actually, adult body mass is difficult to define
because the mass of most passerines fluctuates sea-
sonally.

To summarize, growth-curve analysis is unsuitable
when resource limitations prevent collection of suf-
ficient and precise data, when disturbances lead to
brood abandonment or growth depression, and when
adult sizes cannot be unequivocally measured. For-
tunately, there are viable alternatives to growth-curve
analysis.

Our studies have consistently indicated that several
simple observed growth statistics are equal, or better,
growth indicators than fitted model parameters (Zach
and Mayoh 1986a, b). These statistics are body-mass
asymptote, and body mass, primary-feather length,
and foot length at or near fledging. They are consis-
tent with each other and with fitted model parame-
ters. Further, they are more readily determined than
fitted parameter values because fewer measurements

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