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Correlation between Sequential Variables: A Reply to Schroeder et al.

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Introduction

Rowe et al. (1994) proposed a dynamic model of condition-dependent optimization strategy that predicts optimal combinations of clutch size and lay date based on an individual's arrival date on the breeding ground and body condition at arrival. The optimal strategy is expected to be the outcome of a trade-off between the benefits of a delay in breeding (i.e., improved body condition, leading to higher clutch size) and the costs of late breeding (lower offspring value). An empirical test of the model should thus involve two key parameters: individual arrival date and body condition at arrival. By radio-tracking arctic-nesting geese, Bêty et al. (2003) tested two specific predictions associated with timing of breeding: (1) after their body condition is controlled for, early-arriving females should experience a longer delay on the breeding grounds (longer interval between arrival and lay date) but still lay earlier than late-arriving ones and (2) after their arrival date is controlled for, females in better condition on arrival should have a shorter delay on the breeding grounds, thus laying earlier than birds in poorer condition (see fig. 1 of Bêty et al. 2003). Although Bêty et al.'s (2003) results were consistent with these predictions, Schroeder et al. (2010) suggest that the statistical approaches used in that study were inadequate. They suggest (i) that correlation and regression analyses on sequentially occurring variables were not sufficient to detect nonrandom relationships in this case and thus (ii) that Bêty et al. (2003) could not support the existence of the individual optimal reproductive strategy.

We demonstrate here that the statistical models used by Bêty et al. (2003) were suitable to investigate the association between arrival time and prelaying duration (delay on the breeding grounds). However, we agree that great care should be taken when examining the statistical significance of a correlation or regression coefficients in models involving arrival date and lay date and that randomization tests offer a better alternative under some circumstances.

Relationship between Arrival Date and Prelaying Duration

Schroeder et al. (2010) argue that late-arriving birds have fewer options for selecting a lay date because of environmental constraints. We do not agree with this interpretation. In most species, late-arriving females can delay breeding as much as early-arriving females and still lay eggs during the breeding season, as commonly seen in species renesting after a failed nesting attempt (e.g., Massey and Atwood 1981; Etterson et al. 2009). In species breeding in highly seasonal environments, such as arctic-nesting geese, the "constraints" outlined by Schroeder et al. (2010)—that is, snow cover, nest site, or food availability—usually constrain early-arriving females' timing of nesting but not that of late-arriving females, as conditions steadily improve over time in spring (Gauthier 1993; Prop and de Vries 1993). The observed delays reported in Bêty et al. (2003; prelaying periods ranging from 0 to 10 days) could be applied to all birds arriving on the breeding grounds. Indeed, if the latest-arriving females had delayed their reproduction by 10 days (i.e., the longest observed delay), they would have initiated breeding in late June/early July, when environmental constraints do not preclude such an option. Consequently, late-arriving birds do not have fewer options to breed because of environmental constraints, and it is thus justified to use correlation or regression analyses to investigate the relationship between arrival date and duration of the prelaying periods.

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If we define lay date, L, as the sum of arrival date, A, and the duration of the prelaying period, D (i.e., $A = L - D$), then the correlation between A and D can be defined as

$$\mathrm{Corr}(A, D) = \frac{\mathrm{Cov}\,(L - D, D)}{\sigma_A \sigma_D} = \frac{\mathrm{Cov}\,(L, D) - \sigma_D^2}{\sigma_A \sigma_D},$$

where Cov represents the covariance and σ the standard deviation. The correlation between A and D could thus be positive ($\mathrm{Cov}\,(L, D) > \sigma_D^2$), negative ($\mathrm{Cov}\,(L, D) < \sigma_D^2$), or null ($\mathrm{Cov}\,(L, D) = \sigma_D^2$), and, contrary to the conclusion of Schroeder et al. (2010), there is no bias in favor of one or the other. We thus believe that other statistical approaches, such as randomization and bootstrapping, are not needed to investigate such associations.

Relationship between Arrival and Lay Date

We investigated the suggestion made by Schroeder et al. (2010) on the statistical approach that should be used to test for the association between arrival and lay date (i.e., randomization tests). This suggestion has merit; however, their arguments must be better qualified. Assuming that $A = L - D$ (see above), the correlation between A and L is

$$\mathrm{Corr}(A, L) = \frac{\mathrm{Cov}\,(A, L)}{\sigma_A \sigma_L} = \frac{\mathrm{Cov}\,(A, A + D)}{\sigma_A \sigma_L} = \frac{\mathrm{Cov}\,(A, D + \sigma_A^2)}{\sigma_A \sigma_L}.$$

If A and D are independent, then $\mathrm{Cov}\,(A, D) = 0$, and thus $\mathrm{Corr}(A, L) > 0$ (i.e., if the delay between arrival and lay date is random, then early-arriving birds will lay earlier, as shown by Schroeder et al. [2010]). However, the concept of strategic adjustment rests on the idea that D is a function of A (Rowe et al. 1994) and thus that $\mathrm{Cov}\,(A, D) \neq 0$. Bêty et al. (2003) found support for this prediction because, after the effect of individual body condition is controlled for, A and D were negatively correlated. In such case, the relationship between A and L can, in theory, be positive, negative, or null. However, one premise of statistics is that the strength of any association should be judged against the likelihood that such association could occur purely by chance. As any eggs laid before female arrival on the breeding grounds cannot be observed by researchers, L must be equal to or greater than A. Thus, the observed lay dates reported by Bêty et al. (2003) could not be assigned randomly to all females, as some birds had not arrived on the breeding grounds when the earliest breeders started laying. In such a case, randomization should be used to determine the statistical significance of a specific correlation or regression coefficient (see Brett 2004 for a detailed analysis of the conditions that can lead to spurious correlations between variables). We reran the analyses presented in Bêty et al. (2003) using such an approach (i.e., randomizing the pairing between A and D, 1,000 permutations, as suggested by Schroeder et al. [2010]). Although doing so slightly changed the reported P values, it did not change any of the conclusions; relationship between A and L: correlation coefficient $r = 0.70$, P changed from .000014 to .001, regression coefficient $b = 0.45$, P changed from .000015 to .021 (see tables 1 and 2, respectively, in Bêty et al. 2003).

Conclusion

Under some circumstances, the use of randomization tests should be preferred when investigating the relationships between sequentially occurring variables such as timing of arrival and lay date in birds. The problem here is to specify the "right" null hypothesis (sensu Brett 2004). Nevertheless, none of the original conclusions presented in Bêty et al. (2003) changed when this approach was used. Finally, contrary to suggestions by Schroeder et al. (2010), we urge researchers to avoid oversimplifying the condition-dependent optimization model by considering only arrival and lay date, as these two parameters are insufficient to examine strategic individual reproductive behavior, and advise researchers to also refer to body condition when examining condition-dependent strategies.

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Literature Cited

Bêty, J., G. Gauthier, and J.-F. Giroux. 2003. Body condition, migration, and timing of reproduction in snow geese: a test of the condition-dependent model of optimal clutch size. American Naturalist 162:110–121.

Brett, M. T. 2004. When is a correlation between non-independent variables "spurious"? Oikos 105:647–656.

Etterson, M. A., R. S. Bennett, E. L. Kershner, and J. W. Walk. 2009. Markov chain estimation of avian seasonal fecundity. Ecological Applications 19:622–630.

Gauthier, G. 1993. Feeding ecology of nesting greater snow geese. Journal of Wildlife Management 57:216–223.

Massey, B. W., and J. L. Atwood. 1981. Second-wave nesting of the

California least tern: age composition and reproductive success. Auk 98:596–605.

Prop, J., and J. de Vries. 1993. Impact of snow and food conditions on the reproductive performance of barnacle geese *Branta leucopsis.* Ornis Scandinavica 24:110–121.

Rowe, L., D. Ludwig, and D. Schluter. 1994. Time, condition, and the seasonal decline of avian clutch size. American Naturalist 143: 698–722.

Schroeder, J., O. Mitesser, and M. Hinsch. 2010. Correlations between sequential timing decisions do not necessarily indicate strategic behavior: a comment on Bêty et al. American Naturalist 176:835–837.

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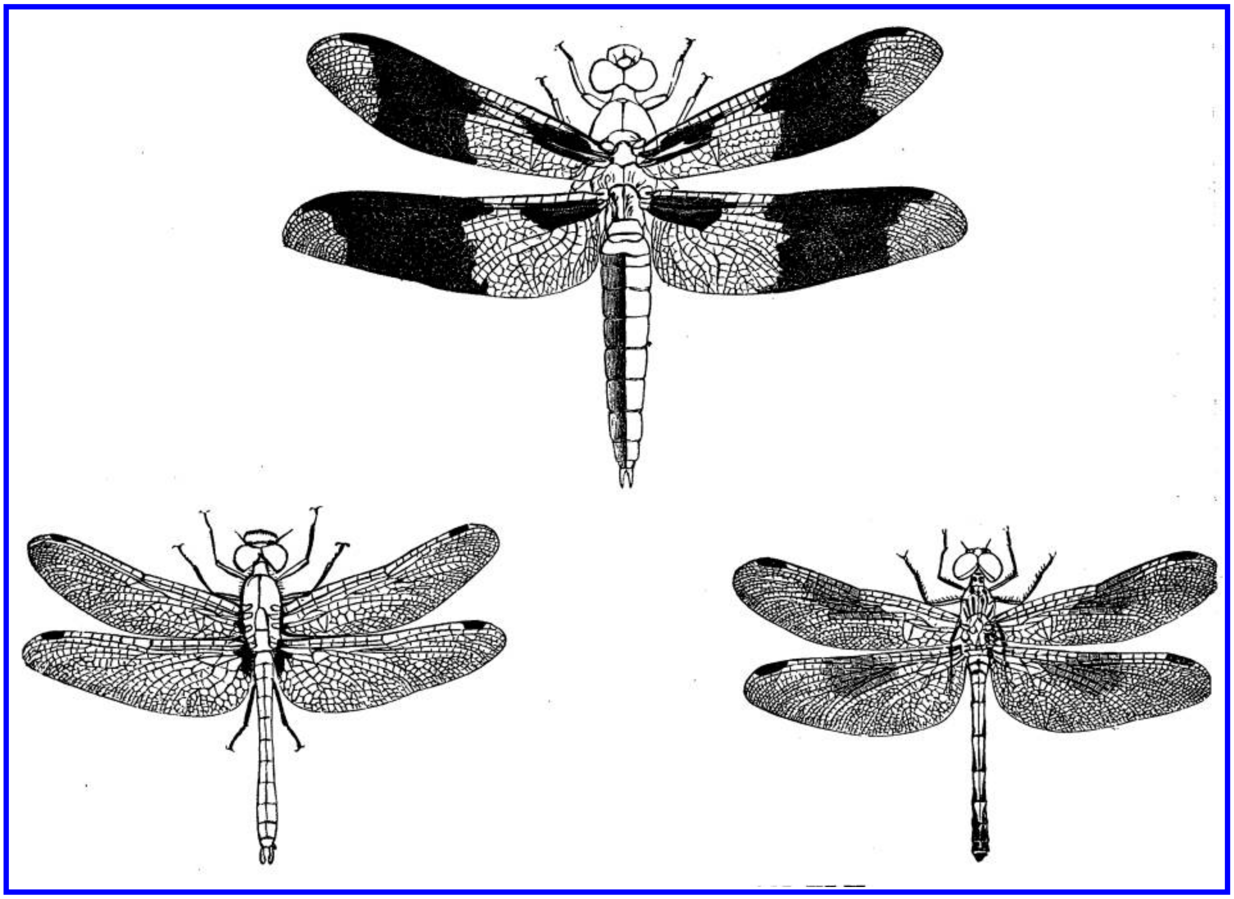

Top, *Libellula trimaculata*, male, "so-called from the three dark clouds on the wings of the female." *Bottom left*, *Diplax berenice*, male. *Bottom right*, *Diplax berenice*, female. "It is black, the head blue in front, spotted with yellow, while the thorax and abdomen is striped with yellow. There are fewer stripes on the body of the male, which has only four large yellow spots on each side of the abdomen." From "The Dragon-Fly," by A. S. Packard Jr. (*The American Naturalist*, 1867, 1:304−313).