The repeatability of variability: exploring intra- and inter-individual variation in seasonality

Animals exhibit seasonal cycles in a variety of physiological and behavioral traits. Studies of these cycles can potentially offer new insights into the evolution of individual differences. For natural selection to act, a trait must be both distinctive within individuals and variable among individuals. The extent to which the amplitude and phase of seasonal cycles fulfill these requirements is not well documented. As a preliminary analysis, we investigated seasonal cycles in the body mass of pigeons, which we weighed quarterly over a period of six years. [Our work with these animals complied with all applicable institutional regulations (University of Groningen Animal Experimentation Committee, license no. 5095) and Dutch and European laws.] We employed several of statistical techniques aimed at 1) quantifying the repeatability of seasonality and 2) comparing within- and among-individual variation in seasonality. Our goal is to take what we have learned from our analyses of mass and apply it to other seasonally variable physiological traits, including variables related to immune function.

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The repeatability of variability: exploring intra- and inter-individual variation in seasonality.

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1. Introduction

BACKGROUND. Animals exhibit seasonal cycles in a variety of physiological and behavioral traits. Studies of these cycles can potentially offer new insights into the evolution of individual differences. For natural selection to act, a trait must be distinctive within individuals and must differ among individuals. The extent to which the amplitude and phase of seasonal cycles (i.e., seasonality) fulfill these requirements is not well documented.

OBJECTIVES.

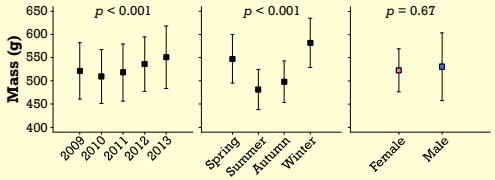
1) Identify important sources of variation, and evaluate whether individuals differ in their overall variability (see *Box 2*).
2) Quantify the repeatability of intra-annual variation (see *Box 3*).
3) Quantify the repeatability seasonal deviation (see *Box 4*).

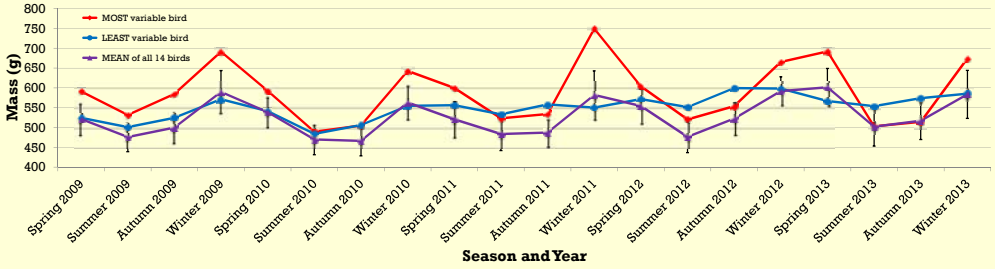
STUDY SYSTEM.

- 14 homing pigeons (*Columba livia*): 6 females, 8 males; all hatched ca. December 2005.
- Quarterly physiological sampling: mass, blood samples, cloacal and choanal swabs.
- Sampled for 5 complete years: spring, summer, autumn, winter in 2009-13 (birds ca. 3-8 years old).

2. Case study: mass

MASS. Individuals changed in mass over time. The effects of season and year were highly significant. The sexes did not differ in mass.

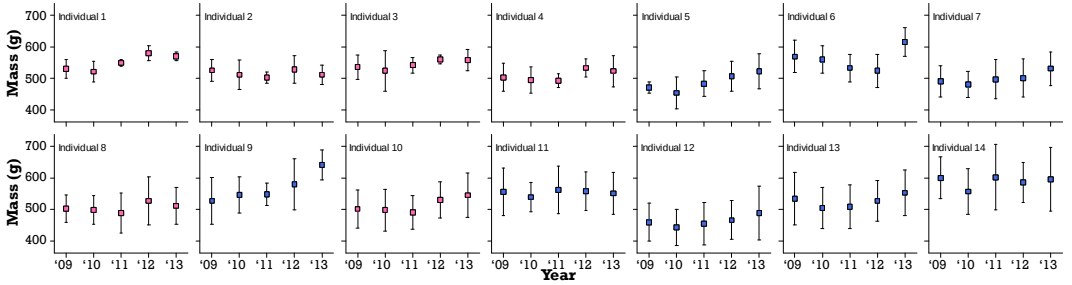




DIFFERENCES IN MASS VARIATION. Individuals differed significantly in terms within-individual variation in mass when tested using either individual standard deviation (iSD) or residual iSD (riSD; mass = year + season) values that were calculated over the entire 5-year period ($F_{19,19} \geq 4.3$, $p < 0.002$).

3. Repeatability of seasonality

MASS AND SEASONALITY *PER YEAR*. First, for each bird, we calculated the mean and the iSD and CV (i.e., seasonality) separately per year. Then, we calculated the repeatability of these values.



HEAVY BIRDS STAY HEAVY. Not surprisingly, individuals' mean mass per year is repeatable.

	$R_{MeanMass}$
Raw	0.65*
Residual (mass = year + sex)	0.80*

VARIABLE BIRDS STAY VARIABLE. More interestingly, individuals' within-year variation is also repeatable.

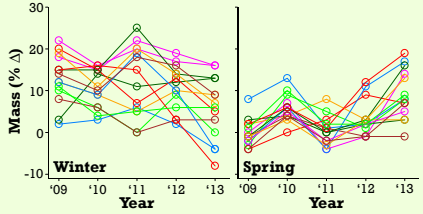
	R_{iSD}	R_{CV}
Raw	0.58*	0.59*
Residual (mass = year + sex)	0.46*	0.48*

*$p < 0.0001$

4. Further analyses & conclusions

The analyses above do not take into account the "source" of the seasonal variation within each year. E.g., is only one season different from the rest? Or are all seasons different from each other?

MASS CHANGE *PER SEASON*. For each bird and each seasonal measurement, we calculated the difference between the seasonal value and that bird's annual mean value (i.e., positive or negative change; in grams and in %). Then per season, we calculated the repeatability of these changes.



	$R_{\%\Delta Winter}$	$R_{\%\Delta Spring}$	$R_{\%\Delta Summer}$	$R_{\%\Delta Autumn}$
Raw	0.42*	<<0.01	0.35*	0.23*
Residual (mass = year + sex)	0.19*	0.02	0.20*	0.36*

*$p < 0.05$

CONCLUSION. Despite categorical effects (e.g., of year, sex) on mass, seasonality is a repeatable trait.
➢ Seasonality overall, winter mass gain, and summer mass loss may be subject to natural selection.
NEXT STEP. We will conduct similar analyses of seasonally variable blood parameters (e.g., [Hp]).

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