

# The Regulation of Behavioral Plasticity by Performance-Based Feedback and an Experimental Test with Avian Egg Production

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**ABSTRACT:** Optimizing plasticity in behavioral performances requires the abilities to regulate physiological effort and to estimate the effects of the environment. To describe how performance-based feedback could play a role in regulating recursive or continuous behavioral performances, I developed two models, one (environmental feedback) that assumes an initial ability to regulate effort but not to predict the effects of the environment and the other (effort feedback) that assumes an initial ability to predict the effects of the environment but not to regulate effort. I tested them by manipulating feedback on egg production, using an egg-substitution experiment in wild, free-ranging Lincoln's sparrows (*Melospiza lincolnii*). I discovered that females adjusted the size of their clutches' third laid eggs in response to the size of an experimentally substituted first laid egg, such that the size of the third laid egg increased with the size of the substitute. Results were largely consistent with the environmental feedback model, though small portions of the response surface were consistent with the effort feedback model or with neither. Regardless, such feedback-based regulation predicted by either model may help females maximize net benefits of egg production and may be a basis for mechanisms regulating a wide range of other behavioral performances, as well.

**Keywords:** egg laying, life-history trait, Lincoln's sparrow *Melospiza lincolnii*, optimal foraging, reproductive effort, unpredictable environment.

## Introduction

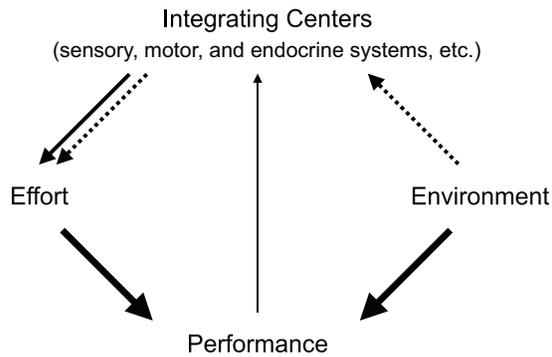
Understanding the proximate factors that regulate plasticity in behavioral performance is of long-standing interest in organismal biology (Piersma and van Gils 2011). An individual's physiological effort plays a role in determining behavioral performance level—the greater the effort, the greater the level of performance—but so too does the environment (Kingsolver and Gomulkiewicz 2003). When the effort imposes fitness costs, the optimal performance should be something less than the maximum of which the individual is capable (e.g., Drent and Daan 1980), and an

individual's ability to target the optimum will thus depend on its ability to predict the cumulative effects of its environment and to regulate effort accordingly (fig. 1).

Some physiological processes recur frequently enough for their behavioral outcomes to provide feedback that helps guide the optimization of subsequent iterations of the process (fig. 1). Such performance-based feedback adaptively shapes the magnitude, timing, or quality of many types of organismal function, from root growth in plants (Eapen et al. 2005) to locomotion in insects (Sane et al. 2007) to vocal communication in vertebrates (Brainard and Doupe 2000). Evidence that birds adaptively adjust the timing of breeding if they had mistimed it according to peak food resources the prior year (Nager and van Noordwijk 1995; Grieco et al. 2002) is consistent with the possibility that performance-based feedback regulates organismal traits on a wide variety of timescales, including those relevant to the individual's life history.

The size of egg a female produces is a performance-based measure of egg production that can influence the size and fitness of the female's young (reviewed in Krist 2011) and can trade off with other life-history traits, such as her clutch size, future reproductive success, and survival (Williams 1966; Stearns 1992). Given this importance of egg size, it is remarkable how little we know about its proximate regulation (Williams 2012). Nonetheless, in the vast majority of bird species, egg production is iterative, raising the possibility that feedback from an initial egg could signal the female how she should optimize the size of later laid eggs. Using optimal foraging theory (Parker and Smith 1990) as a foundation, I propose two models for how performance-based feedback from an initial egg could signal the female either her egg production effort or the cumulative effects of the environment on egg production and thus contribute to the proximate regulation of the size of later laid eggs. In principle, the models could apply broadly beyond egg size regulation to the optimization of many behavioral performances, if those performances incur fitness costs (and therefore have optimal levels) and are recursive or continuous. I

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**Figure 1:** Effort and the environment as two broad categories of proximate factors that affect plasticity in behavioral performance. With all else equal, a change in effort will change performance, as will a change in the environment, broadly defined (thick solid arrows). Physiological systems—such as sensory, motor, and endocrine systems (integrating centers)—regulate effort based in part on input from the environment. However, these centers integrate environmental information and regulate effort imperfectly relative to the optimal performance from a fitness perspective (dotted arrows). In some cases, performance may provide feedback (thin solid arrow) on either effort or the effects of the environment so that on subsequent iterations of the behavioral process, integrating centers may more closely optimize performance by modulation of effort accordingly (medium solid arrow).

then test contrasting predictions of the models with a field experiment involving the manipulation of egg size feedback.

Below I describe the two models for both the natural and the experimental situation, making reference to figure 2. Also, for viewers with (supplementary material, available online) and without (videos 1–4, available online) access to Mathematica, I provide dynamic animations of each model for both the natural and experimental situations.<sup>1</sup>

#### Model Assumptions

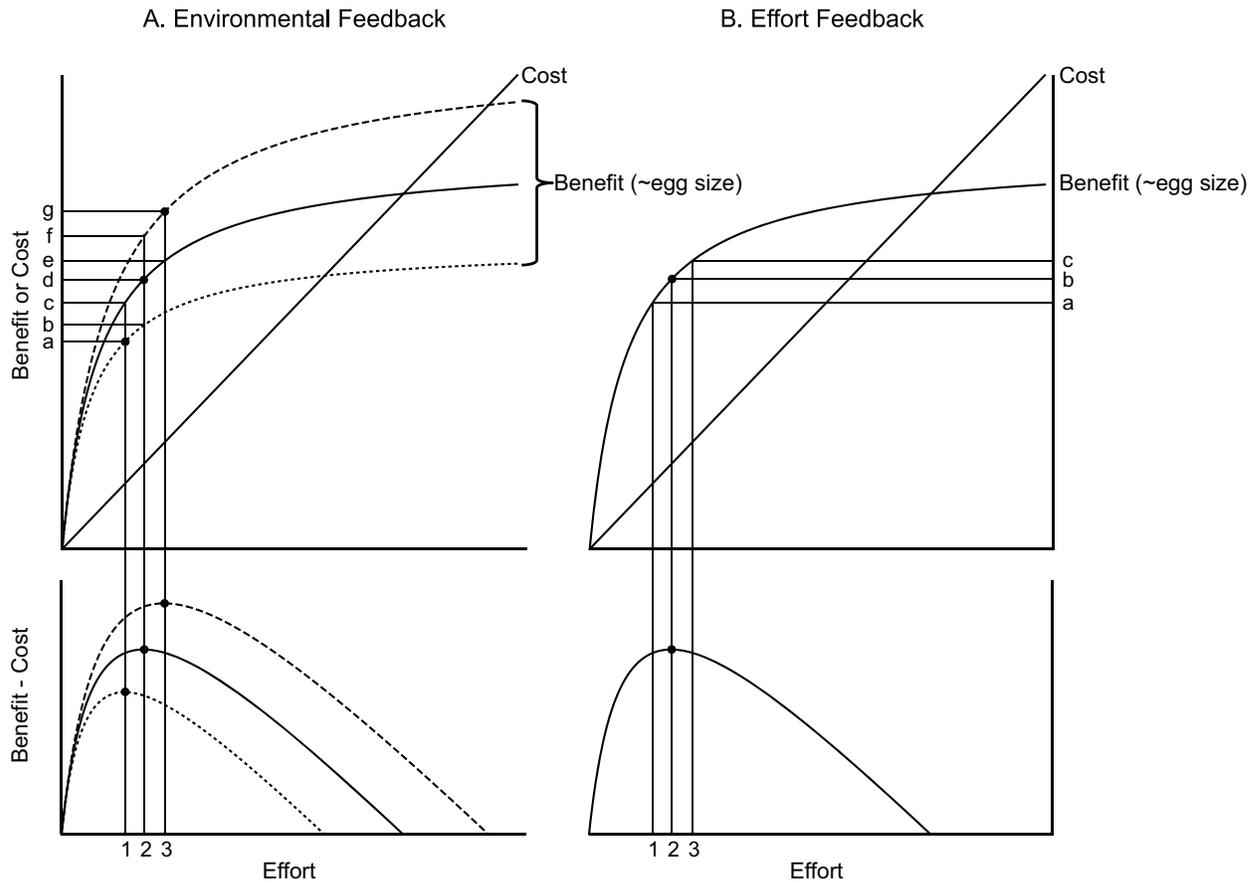
I assume that the benefits of egg production are reflected by the egg's size and that two broad categories of factors proximately influence plasticity in egg size—egg production effort (e.g., foraging time, energy diverted to egg production from other physiological processes) and the environment (e.g., forage quality, climate, predation risk, learning and experience; McGinley et al. 1987; reviewed in Christians 2002). I assume that the benefit of egg production (i.e., egg size) is a monotonic, diminishing function of egg production effort (Smith and Fretwell 1974) and has some optimum (i.e., there exists a maximal difference between the benefit and cost of the effort; fig. 2). I also assume that

changes in the environment affect egg size by changing the slope of the relationship between effort and benefit (separate benefit functions in fig. 2A). Finally, although fitness costs would play an ultimate role in the optimization of egg size (fig. 2), they would not proximately determine egg size and would therefore not be signaled by feedback that is performance based. Thus, I assume that whatever the cost function is, it does not change and is predictable by the individual.

#### Model Predictions and Contextual Example

I propose two models that yield contrasting predictions (fig. 2). Under one, which I call the environmental feedback model (fig. 2A), the laying female can initially facultatively regulate egg production effort but cannot initially predict the effects of the environment. Feedback from an initial egg production performance signals environmental effects, enabling her to optimize the size of later laid eggs. Under the other, which I call the effort feedback model (fig. 2B), she can initially predict the effects of the environment but cannot initially regulate her egg production effort. In this case, the feedback from an initial egg production performance signals her egg production effort, enabling her to fine-tune that effort such that she can optimize the size of later laid eggs. Under the environmental feedback model, if the female under- or overestimates the optimal size of an initial egg, then a later laid egg should be, respectively, proportionally larger or smaller than the initial egg (for reasoning, see contextual example below), and these two alternatives are signaled by the female's initial performance, that is, her initial egg size. Under the effort feedback model, if the female under- or overestimates the optimal size of an initial egg, then a later laid egg should be, respectively, proportionally smaller or larger than the initial (for reasoning, see contextual example below), again signaled by the female's initial performance. Of note is that the two models are opposite in the directions of these predictions and should therefore be readily distinguishable when subjected to an experimental manipulation of performance-based feedback. Moreover, these predictions are robust to changes in the benefit and cost functions, as long as those changes do not violate the assumptions. For example, a benefit function that asymptotes higher, with a shifted inflection point, or even of a sigmoidal shape will still yield the above predictions, as will a cost function that is steeper, shallower, or curvilinear. Moreover, I make no assumptions that an individual's use of one model over the other would necessarily be fixed or flexible; either model could apply, depending on the system or even the conditions. For example, the degree to which relevant environmental parameters vary might favor—in real time or in evolutionary time—an individual's use of one model over the other.

1. Code that appears in the *American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.



**Figure 2:** Modeling the regulation of recursive behavioral plasticity, using avian egg production as an example. *A*, Under the environmental feedback model, the laying female can initially regulate egg production effort but cannot initially predict the effects of the environment. Feedback from an initial egg signals environmental effects and thus how to optimize the size of later laid eggs. Effort values of 1, 2, and 3 are those that maximize the net benefit (benefit – cost) curves for the dotted, solid, and dashed benefit functions, respectively. Benefit values of a–g reflect various egg sizes for each effort value, depending on which benefit function applies. For example, a female that initially thinks the solid benefit function applies should apply an effort of 2. This will result in an egg of size d if she is correct, of larger size (e.g., f) if the environment is better than expected, and of smaller size (e.g., b) if it is worse. If the initial egg is size f, the effort for a later laid egg should be 3 (which maximizes net benefits of the dashed line), yielding a later laid egg of size g. If the initial egg is size b, the effort for a later laid egg should be 1 (which maximizes net benefits of the dotted line), yielding a later laid egg of size a. If a female is experimentally tricked to think that the environment is better than expected (i.e., when her first laid egg of size d is substituted with one of size f), then the resulting effort 3 should yield a later laid egg of size e because the size of the female’s first laid egg should, on average, provide the correct point of intersection with any effort. The same logic applies when the first laid egg is experimentally replaced by one of size b. *B*, Under the effort feedback model, the female can initially predict the effects of the environment but cannot initially regulate her egg production effort. In this case, feedback from an initial egg signals her egg production effort and thus how to fine-tune that effort such that she can optimize the size of later laid eggs. Effort 2 is that which maximizes the net benefit curve for the benefit function and yields a benefit (egg size) of b. A female that initially underestimates or overestimates the optimal effort (e.g., efforts 1 and 3, respectively) produces an egg that is too small or too large, respectively. For example, if egg 1 is size c, she should reduce effort in order to optimize the size of a later laid egg (size b). If a female is experimentally tricked to think that her effort was 3 (i.e., when her first laid egg of size b is substituted with one of size c), she should reduce effort using her actual effort (2) as the starting point and produce for a later laid egg an effort of 1 and thus a later laid egg of size a. The same logic applies when her first laid egg is replaced by one of size a. Circles indicate the optimum value for each benefit and net benefit curve. Dynamic animations of each model for both the natural and experimental situations are provided to viewers with access to Mathematica (supplementary material, available online) and to viewers without access to Mathematica (videos 1–4, available online).

To put each model into context, assume that time spent foraging during egg production is an accurate measure of egg production effort: the greater the effort, the greater the time, the greater the size of the egg, and thus the greater

the benefits of egg production. This greater foraging time would also incur a fitness cost, such that there exists some optimal time that maximizes the net benefits (benefit – cost) of egg production (fig. 2, bottom); time in addition

to the optimum yields a larger fitness benefit but at an even greater fitness cost, and time less than the optimum yields a reduction in fitness cost but an even greater reduction in fitness benefit.

For the environmental feedback model, suppose that changes in the environment that affect egg size do so by affecting forage yield and thus energy consumed, assimilated, and converted per unit time (effort) foraging. For a single level of foraging time, forage yield could be high, providing much energy to convert to an egg, resulting in a large egg (fig. 2A, top benefit function). Alternatively, forage yield could be low, providing little energy to convert to an egg, resulting in a small egg (fig. 2A, bottom benefit function). Or foraging yield could be somewhere in between (fig. 2A, middle benefit function). If the female's initial foraging time (fig. 2A, effort 2) reflects an underestimate of the optimum for the true forage yield (i.e., she thinks the middle benefit function applies, when, in fact, the top benefit function applies), her initial egg (fig. 2A, benefit f) will be larger than expected (fig. 2A, benefit d), signaling the need to increase foraging time (fig. 2A, effort 3) during the production of later laid eggs in order to target the optimum (fig. 2A, benefit g) for the environment (fig. 2A, top benefit function). If the female's initial foraging time reflects an overestimate of the optimum for the true forage yield (i.e., she thinks the middle benefit function applies, when, in fact, the bottom benefit function applies), her initial egg (fig. 2A, benefit b) will be smaller than expected, signaling the need to reduce foraging time (fig. 2A, effort 1) during the production of later laid eggs in order to target the optimum (fig. 2A, benefit a) for the environment (fig. 2A, bottom benefit function). Although I use a change in forage yield for my example, a myriad of environmental changes (e.g., energy type of forage, energy amount per unit forage, climatic conditions affecting the egg producer's metabolic rate or allocation of energy) could affect the conversion of egg production effort to an egg and thus the optimal egg size. But not any type of environmental variability is relevant. The rate at which the environmental factor changes should not be so high that it renders the feedback obsolete. For example, if change in forage yield is too rapid and unpredictable so as to render feedback outdated, then behavioral adjustments based on this feedback would not help.

For the effort feedback model, in which the effects of the environment are assumed to be stable or predictable, feedback based on the size of the first egg would signal her initial foraging effort and the direction and degree to which she should alter it for later laid eggs (fig. 2B). If the female's initial effort reflects an underestimate (fig. 2B, effort 1) of the optimum foraging time (fig. 2B, effort 2; i.e., she thinks she is applying effort 2, when, in fact, she is applying effort 1), her initial egg (fig. 2B, benefit a) will be smaller than expected (fig. 2B, benefit b), signaling the need to ele-

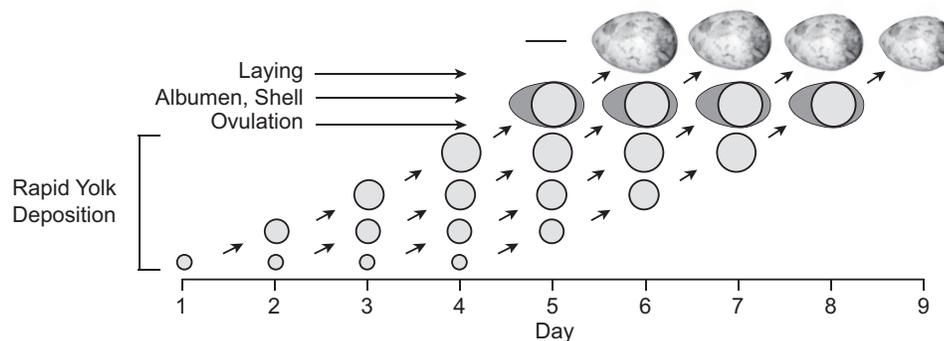
vate foraging time during the production of later laid eggs in order to target the optimum (fig. 2B, benefit b). If the female's initial effort reflects an overestimate (fig. 2B, effort 3) of the optimum foraging time (i.e., she thinks she is applying effort 2, when, in fact, she is applying effort 3), her initial egg (fig. 2B, benefit c) will be larger than expected, signaling the need to reduce foraging time during the production of later laid eggs in order to target the optimum.

One can think of the two models using target shooting as an analog. Under both models, the goal is to hit the target. Under the environmental feedback model, initially the female may be able to aim well, but she does not know where the target is until her first shot reveals it. Under the effort feedback model, she knows where the target is but does not know how she is aiming until her first shot reveals that aim. Both the environmental feedback and the effort feedback models would require the capacity for very rapid egg size regulation guided by tactile or visual input from an initial egg and may reveal one way females assess and optimize plasticity in many recursive or continuous behavioral performances—through performance-based feedback.

#### Experiment Approach

Using a wild, free-ranging population of Lincoln's sparrows (*Melospiza lincolnii*), I tested the hypothesis that cues from the first laid egg affect the size of later laid eggs within a clutch, and in order to distinguish between the two models, I examined the direction of any change relative to the size of the first laid egg. As in most passerine bird species (Johnson 1996; but see Badyaev et al. 2006), it is assumed for Lincoln's sparrows that once an ovarian follicle is recruited into the hierarchy of growing follicles, rapid yolk deposition proceeds over 4–5 days, after which the ovum is ovulated (fig. 3). As the ovum passes through the oviduct, albumen and shell are deposited around it over the next 24 h, after which it is laid about an hour before the next ovum is ovulated (Skutch 1952). Thus, within about an hour of the female's first visual or tactile input from her first laid egg, the second ovum is in the oviduct and the yolks for eggs 3 and 4 are developing on the ovary. This process yields the laying rate observed in most bird species, including the Lincoln's sparrow, of one egg per day (each laid by 0730 hours local time in this study population) until the clutch is complete (at a modal clutch size in Lincoln's sparrows of four eggs [Sockman 2008]).

On the day they were laid, I substituted the first egg of one female with an egg from another female and repeated this for additional females as we found appropriately scheduled nests and their eggs became available. Females were allowed to lay and retain later laid eggs in the clutch.



**Figure 3:** Egg formation in birds. Once recruited into the follicular hierarchy (smallest gray circles), a follicle undergoes 3–4 days (in Passeriformes) of rapid yolk deposition, after which it is ovulated. The albumen and shell are added in the oviduct over ~24 h, after which the complete egg is laid at approximately the same time the next ovum is ovulated (days 6–8). This continues until the clutch is complete (in this case, with four eggs). In the egg substitution experiment, the first laid egg was replaced with a substitute on the day they were laid and therefore just after the ovum of the second egg would have been ovulated and when the follicles for eggs 3 and 4 would have been undergoing rapid yolk deposition. Variation in egg size relative to laying order depicted at the top reflects the relative range of egg size variation observed in this study, although within natural Lincoln’s sparrow clutches, egg size varies little with respect to laying order (Sockman 2008). Scale bar = 1 cm (for complete eggs).

This procedure constituted an experimental perturbation of performance-based feedback on egg production, in that, because of a size differential between the first laid egg and its substitute, each female received tactile and visual feedback from the substitute egg that varied about the feedback she would have experienced naturally from her own egg.

Predictions for this experimental situation differ from the natural situation described above for the following reasons. On average, the size of the first laid egg should reasonably well reflect the optimal effort for the true cumulative effects of the environment. The first laid egg of an individual female may vary from her optimum, but to the extent that one female overestimates her environment or optimal effort, another female should underestimate it. In the natural situation, feedback from the first laid egg cues the female to the true effects of her environment or her effort (according to the models). But in the experimental situation, that first laid egg is substituted with feedback that varies about the true effects of her environment or about her true effort, thereby tricking the female into thinking that either her environment or her egg production effort is something it is not. If she adjusts effort for later laid egg production according to the environmental feedback model, that new level of effort will interact with her actual environment, that is, with the one reflected by her first laid egg, not any sort of perceived environment reflected by the substitute. In other words, the benefit function relevant to the later laid egg is that defined by the first laid egg (i.e., the middle function in fig. 2A). If the female adjusts effort for later laid egg production according to the

effort feedback model, that new level of effort will be adjusted according to the effort required to produce her first laid egg, not according to the effort required to produce the substitute.

As a result, predictions from the environmental feedback model differ in two ways from those of the effort feedback model. First, they differ in terms of which of the three eggs—first laid, substitute, or later laid—should be the middle sized. Under the environmental feedback model, the size of a later laid egg (fig. 2A, benefits c and e) should fall, on average, somewhere between the size of the first laid egg (fig. 2A, benefit d) and the size of the substitute (fig. 2A, benefit b if later laid egg is benefit c and benefit f if later laid egg is benefit e). Under the effort feedback model, the size of the first laid egg (fig. 2B, benefit b) should fall, on average, somewhere between the size of later laid eggs (fig. 2B, benefits a and c) and the size of the substitute (fig. 2B, benefit a if the later laid egg is benefit c and benefit c if the later laid egg is benefit a). Second, they differ in terms of the sign of the coefficient for the size of the substitute egg used in statistical equations to predict the size of the later laid egg. Under the environmental feedback model, that coefficient should be positive; that is, the size of the later laid egg should increase with size of the substitute. Under the effort feedback model, the coefficient should be negative; that is, the size of the later laid egg should decrease with the size of the substitute. Thus, even when performance-based feedback is experimentally manipulated, the two models oppose one another in two sets of predictions and should therefore be distinguishable.

## Material and Methods

### *Study Site and General Field Procedures*

Field assistants and I collected data for this study during the 2007–2009, 2011, and 2015 Lincoln's sparrow breeding seasons at Molas Pass, Colorado (37.74°N, 107.69°W). At an elevation of 3,250 m, the study site is a subalpine, wet meadow approximately 20 ha in area (Sockman 2008, 2009).

We found nests by searching appropriate habitat. We marked eggs as they were laid, and after at least 2 days had passed with no additional eggs, we recorded clutch size, measured each egg's length and width with dial calipers, and calculated egg size (i.e., volume) following Hoyt (1979).

Despite a robust population with an estimated 40–80 nesting pairs per season (there was a total of 243 nests found during the years of this study), a few factors constrained the sample size of egg substitutions used in analyses. First, I used only four-egg clutches in the analyses (see below). Second, nests were sometimes depredated before we measured eggs, or, for reasons that were often unknown, females sometimes abandoned their nests, especially during laying when they seemed most prone to abandoning. Third, as indicated above, I always substituted eggs on the day the substitute and first laid eggs were laid, and consequently only the small subset of nests found before or during laying were applicable. Fourth, onset of laying is highly asynchronous in this population, occurring anytime over a period of approximately 45 days between early June for the earliest females and mid-July for the latest females. Although we may have found a nest in time to observe the first egg on the day it was laid and therefore substitute it, we may not have found another nest that also had an egg laid that day and which we would need for the substitution. Therefore, egg substitutions—requiring the fortuitous discovery of two appropriately synchronized four-egg nests early in their cycles and which were not abandoned or depredated before clutch completion and egg measuring—were infrequent, necessitating several seasons in order to yield a sufficient sample size (2007: 4 nests; 2008: 5 nests; 2009: 3 nests; 2011: 6 nests; 2015: 6 nests). Sometimes the substitute was larger than the first laid egg (13 nests), and sometimes it was smaller (11 nests). Sometimes the size difference between the substitute and first laid egg was large, and other times there was little difference between eggs (range: 0.05%–26%; mean: 8.6%). However, the size difference was never something over which I had any control. Which nests and therefore which eggs I used in a substitution were based on the natural, seemingly random vagaries of the population's nesting phenology and our ability to find nests in time. On the rare occasion when more than two nests at a time were available for egg substitutions, I selected those closest to one another in order to minimize the transport time of the

eggs. All substitutions occurred between 1001 and 1524 hours local time and thus after ovum 2 would have been ovulated. Each female laid one egg per day, except for one that skipped a day between the first and second eggs and which I therefore excluded from analyses.

### *Analytical Considerations*

In order to eliminate clutch size as a source of variation, all analyses used four-egg clutches only. It should be noted, however, that low variability in clutch size (one three-egg clutch, 24 four-egg clutches, and five five-egg clutches) precluded statistical analyses of the effects of my experiment on clutch size but also suggested a lack of any strong effect, as might otherwise be predicted by life-history theory (e.g., Williams 2001).

Facultative egg size modulation is well documented in birds (Williams 1996; Cunningham and Russell 2000; Schaper and Visser 2013) and can sometimes be very rapid (Dentressangle et al. 2008), but it was not clear from previous studies or from theory in which of eggs 2, 3, or 4 I might observe a response. If my hypothesis is correct and females can respond rapidly, then there is no reason to think that females should use feedback from only egg 1; egg 1 could affect the size of egg 2, egg 1 and 2 could affect the size of egg 3, and eggs 1–3 could affect the size of egg 4 (see fig. 3). In the experimental situation, feedback from eggs 2 and 3, which were not substituted, would counter that from the substitute (fig. 2). This would reduce my ability to observe an effect of the substituted egg on eggs 3 and 4, possibly leaving only egg 2 to show a robust response. However, a response in egg 2 would require the size regulation to occur in the oviduct, which, to my knowledge, has not previously been shown for any type of facultative egg size modulation in a bird. On the other hand, if responses to feedback are slower, females may be able to mobilize a response to egg 1 only in eggs 3 or 4 but not in egg 2. Because of these uncertainties, I analyzed responses in each of the three later laid eggs.

### *Statistical Analyses*

Prior to testing predictions of the models, I first examined whether my experimental manipulation affected the size of later laid eggs, using three simple linear regressions (one for each of eggs 2–4,  $N = 24$  for each) in which size of the substitute egg was the predictor. Subsequent analyses explicitly tested model predictions.

Although the relative role of the actual environment or effort (estimated by the size of the first laid egg) and the simulated environment or effort (estimated by the size of the substitute egg) will depend on the details of the true relationship between effort and egg size and the true effect of

the environment, both models predict a simple additive effect of the size of the first laid egg and the size of the substitute (fig. 2). Moreover, distinguishing between the two alternative models requires a parameter estimate not only for the substitute egg but also for the first laid egg (see above and below). Therefore, I analyzed the response of eggs 2–4 each in a separate multiple linear regression, with the size of the first laid egg and the size of the substitute egg as the predictors (each model:  $N = 24$  clutches). Including the size of the first laid egg in statistical analyses served an additional function as well. Because of their common environment and other factors, the size of the first laid egg could be correlated with that of the substitute and those of its later laid sibling eggs, leading to a spurious effect of the substitute on later laid eggs. Inclusion of this covariate controlled for this possibility, even though the correlation between the first laid egg and substitute egg, in reality, was quite weak (correlation coefficient = 0.22,  $P > .2$ ,  $N = 24$ ).

For the one regression model with strong statistical support (egg 3; see “Results”), I then examined consistency with the environmental feedback model relative to the effort feedback model and relative to neither model. To do this, I first noted the sign of the coefficients for the sizes of the first laid and substitute eggs. As stated above, the environmental feedback model predicts a positive coefficient for the size of the substitute egg, whereas the effort feedback model predicts that coefficient to be negative. A negative coefficient for the size of the first laid egg or coefficients for the sizes of either the first laid or the substitute egg that are not significantly different from 0 would support neither model. Also as stated above, the models differ in terms of which of the three eggs should be the middle sized. Under the environmental feedback model, it should be the later laid egg, and under the effort feedback model, it should be the first laid egg. Neither model is predicted by the third possibility, that the substitute egg is the middle sized. To examine these alternatives, I generated a graphical depiction of the three-dimensional response surface, using the model’s parameter estimates, and I shaded the regions of the surface consistent with each or neither model. I then randomly selected 10,000 points on the response surface by randomly generating values for the first laid egg, pairing each with a randomly generated value for the substitute egg, and calculating the response of the later laid egg with the model’s parameter estimates. I generated the random values using two approaches. In the first, I drew from a uniform distribution between the range of egg size values observed naturally for the first laid and substitute eggs. In the second, I drew from a normal distribution using the mean and standard deviation observed naturally for the first laid and substitute eggs. I then counted the frequency of points consistent with each or neither model and used a

goodness of fit test to determine the probability that these frequencies could have resulted from chance alone.

## Results

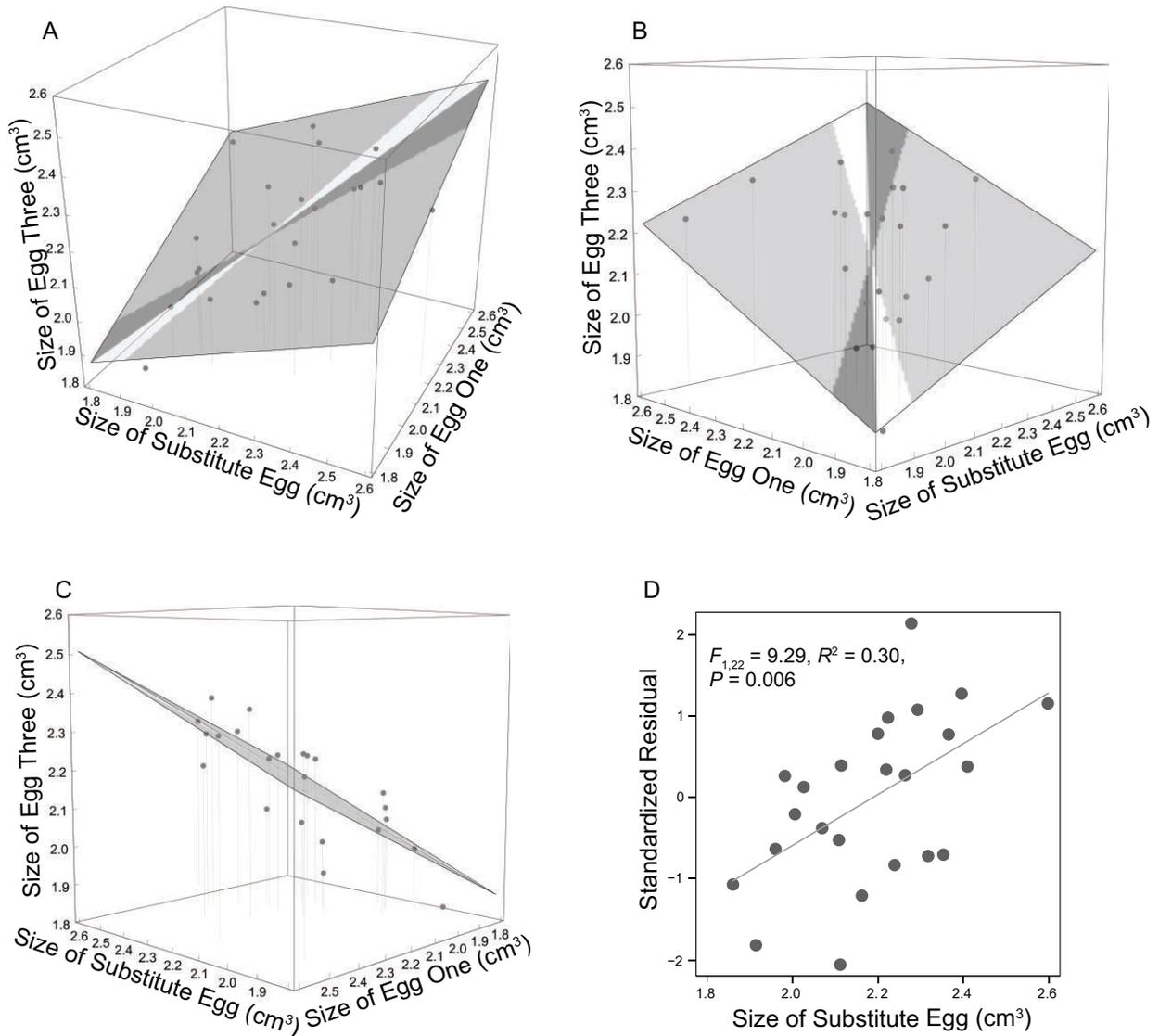
I found that the size of the substitute egg affected the size of the female’s third laid egg, regardless of whether (table 1; fig. 4) or not (egg 3:  $F_{1,22} = 9.98$ ,  $R^2 = 0.31$ ,  $P = .005$ ) I included the first laid egg as a covariate in models. Additionally, the size of her first laid egg predicted the size of egg 3 (table 1; fig. 4). In other words, females changed the size of egg 3 in response to the size of the substitute, and the size of egg 3 was also correlated with the size of the first laid egg (fig. 4). Statistical support for these effects on the size of eggs 2 and 4 was marginal at best, regardless of whether (table 1) or not (egg 2:  $F_{1,22} = 3.34$ ,  $R^2 = 0.13$ ,  $P = .08$ ; egg 4:  $F_{1,22} = 3.74$ ,  $R^2 = 0.15$ ,  $P = .07$ ) I included the first laid egg as a covariate in models.

For the response with strong statistical support (egg 3), results were strongly supportive of the environmental feedback model over the effort feedback model or over neither model. Coefficients for both the first laid egg and the substitute egg were positive and therefore consistent specifically with the environmental feedback model but not with the effort feedback model or with neither model. Additionally, the shading of the egg 3 response surface for the model defined by the coefficients in table 1 indicated a strong majority of support for the environmental feedback model, in which the later laid egg (egg 3) was the middle sized of the three eggs (fig. 4). There were some areas of the response surface, albeit considerably smaller, that were consistent with the effort feedback model and still others that were also smaller in area and that were consistent with neither model. Of the 10,000 randomly selected points from a uniform distribution on the egg 3 response surface, 8,184 (82%) fit the

**Table 1:** Statistical effects of the sizes of the first laid and substitute eggs on the size of later laid eggs

Predictor	Estimate	SE	<i>t</i>	<i>P</i>
Size of egg 2:				
Intercept	.852	.246	3.47	.002
First laid egg	.470	.092	5.13	<.001
Substitute egg	.131	.089	1.48	.154
Size of egg 3:				
Intercept	.438	.325	1.35	.191
First laid egg	.440	.121	3.64	.002
Substitute egg	.356	.117	3.04	.006
Size of egg 4:				
Intercept	.828	.394	2.10	.048
First laid egg	.420	.147	2.86	.009
Substitute egg	.219	.142	1.54	.139

Note: Analyses are multiple linear regressions. Egg size is in cubic centimeters. Sample size for each of the three analyses is 24 clutches.



**Figure 4:** A–C, Effects of the sizes of the first laid and substitute eggs on the size of egg 3, showing three perspectives of the response surface. Areas consistent with the environmental feedback model (light gray), the effort feedback model (dark gray), and neither model (white) are shown. D, Effect of the size of the substitute egg on the standardized residual from a linear regression of the size of egg 3 on the size of the first laid egg.

environmental feedback model, 914 (9%) fit the effort feedback model, and 902 (9%) fit neither. With a normal distribution as the basis for the randomly drawn points on the response surface, 8,672 (87%) fit the environmental feedback model, 717 (7%) fit the effort feedback model, and 611 (6%) fit neither. The probability that either combination and more extreme combinations of frequencies was a result of chance alone was very small (uniform distribution:  $\chi^2 = 10,588$ ,  $df = 2$ ,  $P < .0001$ ; normal distribution:  $\chi^2 = 12,827$ ,  $df = 2$ ,  $P < .0001$ ). Data underlying the results are

deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.4bq4q> (Sockman 2015).

### Discussion

There are two principal conclusions from this study. The first is that a female bird can modulate the size of an egg on the basis of cues from a previously laid egg. I found that a substitute of the first laid egg of a clutch affected the size of the third laid egg. To my knowledge, such rapid faculta-

tive modulation of the size of an egg already in the process of formation (fig. 3) and specifically in response to the size of an egg laid earlier in the sequence of clutch formation has not previously been demonstrated. Size changes in the third egg may have been due to changes in yolk volume, albumen, or shell thickness, but the mechanistic basis of this feedback-based egg size regulation is unknown. Nonetheless, the possibility that visual or tactile cues from an already laid egg trigger an endocrine or paracrine response that then modulates allocation to later laid eggs is a reasonable hypothesis based on work in other avian (Williams 2001) and nonavian (Sinervo and Licht 1991) vertebrates.

Second, the results were largely consistent with one of the two competing models I proposed, the environmental feedback model. That is, the coefficients for the model's two predictors were both positive, and the great majority of the response surface indicated that the later laid egg was the middle sized of the three (fig. 4), which was what this particular model predicted and which is what set it apart from the alternative, effort feedback model, which predicted a negative coefficient for the size of the substitute egg and that the first laid egg would be the middle sized (fig. 2). Thus, results are consistent with the hypothesis that a female bird modulates the size of an egg according to feedback from a previously laid egg on the cumulative effects of the environment. That said, a small proportion of the response surface was consistent with the effort feedback model, and another small proportion was consistent with neither model. However, it is not clear the extent to which support for the effort feedback model and neither model was a result of error in the estimates of the parameters used to generate the response surface (table 1). Of course, there is some degree of error across the entire response surface due to error in the parameter estimates, but the degree to which that error raises uncertainty in which model is supported depends both on the magnitude of the error and on the particular location on the response surface. A small change in the size of the first laid egg or substitute egg near their identity line will cause wholesale change in which model is supported, whereas in other regions of the surface, the same degree of change in these two predictors will not affect which model is supported. Consequently, it is not surprising that the region in which I observed the most variation in model support immediately flanked the region where the size of the first laid egg equaled that of the substitute egg.

Although results from this study on the manipulation of egg size feedback support one model over the other, other types of behavioral performance perhaps in other systems might best be explained by the other model. Or, the same type of behavioral performance (egg production) in the same system (this study population of Lincoln's sparrows) but under different environmental conditions might best be explained by the other model. For example, under highly

stable or predictable environments or for behaviors less susceptible to environmental influences, the effort feedback model or neither model may be supported. In the particular environment at the time of this study, where physical, ecological, and social environmental conditions can be variable and unpredictable (Sockman 2009), having a mechanism such as that hypothesized in the environmental feedback model would seemingly help females minimize maladaptive egg size variation (Christians 2002) through better targeting of the true relationship between egg production effort and egg size for the particular conditions under which they are laying. Although I was unable to examine the effects of the experiment on offspring size, such facultative changes in egg size are expected to affect offspring size because of the influence yolk and albumen volume can have on offspring size in birds and other vertebrates (Freeman and Vince 1974; Finkler et al. 1998; Warner and Lovern 2014).

Before the effects of any feedback, one might expect both the imperfect regulation of effort and the imperfect estimation of environmental effects on that effort, and therefore one might ask whether both models simultaneously apply in some situations. This seems unlikely, because their predictions oppose one another. Indeed, the hypothetical framework, as I have presented it, fails when individuals can neither regulate effort nor predict the environment at the outset, because feedback would simultaneously signal to increase effort on the basis of one model and decrease effort on the basis of the other. Thus, to the extent that either model is accurate, another conclusion is that either an individual must have some degree of regulatory control over its initial effort or it must not respond to or not experience unpredictable environmental conditions that impinge on that effort. Alternatively, some other yet to be conceived model might provide a suitable framework for the proximate regulation of behavioral performance based on environmental and effort feedback. It is hard to conceive how a single form of feedback (in the case of my model, it is the size of the egg) could provide both forms of feedback, but perhaps feedback from one source (e.g., egg size) could provide feedback on the environment and feedback from another source (e.g., some sort of internal physio-stat) could provide feedback on effort.

Additionally, there are some caveats to consider. I intended the egg substitution experiment to dissociate the size of the first egg a female laid from the size she perceived she laid. Nonetheless, female Lincoln's sparrows may have perceived something else instead, specifically that the substitute was a possible parasite warranting a response that might curb its advantage. One such response would be to alter the normal pattern in which egg size does not change with laying order (Sockman 2008), by increasing the size of the parasitic egg's competitors (i.e., later laid eggs), analogously

to the way that other parasite hosts marginalize eggs perceived as potentially parasitic (Lyon 2003). However, the particular way in which females in the present study altered the size of later laid eggs is not consistent with this alternative. To best compete with a substitute egg perceived as parasitic and which is larger than the first laid egg, later laid eggs should have been at least the size of the parasite, not something short of it, as the environmental feedback model predicts and results from this experiment predominantly support. Although the opportunity to elevate egg size in eggs 2 and 3 may have been limited, females had more time to elevate egg size further in egg 4, yet they did not. When the substitute was smaller than the first laid egg, generally the response was to reduce egg size, which also seems counterintuitive as a strategy for coping with a parasitic egg. Rather, the responses in eggs 2–4, when taken together, are more consistent with the use of performance-based feedback in the estimation of the true relationship between egg production effort and egg size and thus in the adaptive regulation of egg size according to life-history predictions. Still, until both parasitism rates and the degree to which females have the ability to change egg size can be determined, the possibility that females were responding as though the substitute were a parasite remains viable.

The models assume that an individual can estimate the function linking three variables—effort, environment, and benefit. An individual may not know the values of all three variables initially upon the first iteration of some behavior, but with feedback on one variable and preexisting knowledge of one other variable and of the function, the models assume an ability to estimate reasonably accurately the third variable. Under the assumption that this is true, there is nonetheless bound to be some error in the feedback signal and in the estimation of the other two variables, raising questions as to how such error might affect predictions about an individual's response to feedback, be it natural or experimentally manipulated. Error would seem most likely to result in noise about the optimal values of any parameter but should not bias the outcome in such a way that, for example, one might draw the incorrect conclusion regarding which, if any, model is being supported by the data. An individual's error may cause him or her to respond incorrectly. However, with replication, that error should be balanced by error from other individuals or from multiple iterations from the same individual such that, on average, the results over a subpopulation should enable one to conclude whether either model is accurate. Additionally, it is important to note that even in the absence of error in the estimation of optimal values for effort and for the environment, a response may still be suboptimal. This is because neither model assumes an ability to account for all variables that might be important in optimizing a behavior. As alluded to above, only certain types of environmental varia-

tion apply to this type of performance-based feedback—the types that are not so rapidly changing or unpredictable that feedback is rendered obsolete before the individual can use it. Thus, depending on the environment, one might still observe a suboptimal behavioral response even in the hypothetical individual that perfectly estimates effort and the environment (using feedback) and thus produces the behavior perfectly predicted by the function linking them.

With all this in mind, findings here suggest some promising avenues of future exploration. For decades, ornithologists have used egg substitutions nearly identical to mine but for another purpose, to test hypotheses concerning hatching asynchrony (experimentally separating the effects of laying and hatching order on offspring growth and survival; Magrath 1990). Insofar as they may have included measures of egg size, these studies should provide an opportunity to examine feedback-based egg size regulation in other systems and without having to conduct additional experiments. Depending on natural history, the dynamics of how individuals respond to feedback could vary; regardless, it is possible that some capacity to use feedback for regulating egg size and other life-history traits is widespread.

As I indicated previously, the models I proposed could apply broadly beyond egg size regulation to the optimization of many recursive or continuous behavioral performances. For example, does a cricket modulate calling effort on the basis of feedback on the frequency with which it attracts a mate? Here, one might imagine that an environmental change that affects sound propagation—such as air temperature—could, for a single stridulation effort, differentially affect mate attraction and therefore differentially affect the relationship between mate attraction effort and its benefits, making acoustic signaling well suited for the effects of performance-based feedback regulation. Autocoprophagic hindgut fermentation seems an ideal opportunity for performance-based feedback on digestion. For example, does a rabbit use chemical and mechanical feedback from the first passage of its food through the digestive tract to modulate digestive secretions and smooth muscle contractile effort during the second pass? Animal migration might also be a fertile field of exploration regarding the potential role of performance-based feedback. Winkler et al. (2014) recently reviewed how vertebrates might adjust migratory decisions according to environmental change. Although their review is not focused strictly on adjustments in migratory effort according to performance-based feedback, it does raise the possibility that changes in environmental conditions—such as wind for fliers or water current for swimmers—could alter the optimal effort necessary to maximize the net benefits of locomotory effort. Hypothetically, feedback might come in the form of visual, olfactory, magnetic, or celestial landmarks that, in conjunction with an internal clock, cue the individual's migratory effort

(flight or swimming speed). One can certainly come up with many more hypothetical examples. Indeed, the models I have proposed for the regulation of egg size in a bird might, in a broad sense, apply to many other recursive or continuous behavioral performances with fitness costs.

Finally, the models I have proposed apply only to feedback on performance and therefore to the proximate regulation of recursive or continuous behavior. Unlike the effects of effort and the environment, the effects of fitness costs of performance, although relevant to the optimization of performance, do not proximately control it. However, there is no reason to assume that such costs would not also be dynamic, unpredictable, and therefore an important factor for any individual adaptively regulating performance. Future models might aid in our understanding of proximate factors that regulate plasticity in behavioral performance by accounting for unpredictable changes in the fitness costs of recursive or continuous behavior, not just changes in the benefits.

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Four-egg clutch in nest of Lincoln's sparrow (*Melospiza lincolnii*). Photograph by M. Pia Rodriguez.