

# Sibling competition and the evolution of prenatal development rates

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Sibling competition has been proposed as an important evolutionary pressure driving interspecific variation in developmental rates. We tested this hypothesis using rates of extra-pair paternity and brood parasitism, as well as the degree of hatching asynchrony, as indices of sibling competition in a comparative analysis of 70 species of bird. We found mixed support for the influence of sibling competition on prenatal development. Brood parasitism was negatively correlated with the length of incubation, and hatching asynchrony was positively correlated with the length of incubation, but both correlations disappeared when phylogeny was controlled for. Extra-pair paternity, however, was negatively correlated with incubation length even when phylogeny was controlled for. The latter could represent support for the influence of sibling competition on prenatal development or indirect effects of correlated selection on both traits by adult mortality. The existence of these correlations demonstrates that life-history strategies include linkages among a larger suite of traits than previously recognized.

**Keywords:** sibling competition; developmental rate; incubation period; extra-pair paternity; life-history evolution

## 1. INTRODUCTION

Developmental rates are an integral component of life-history strategies and vary tremendously among species. For example, the incubation period can vary more than three-fold among birds with similarly sized eggs (Rahn & Ar 1974). Such extensive variation in the time required to complete development is somewhat of a paradox because most selection pressures are presumed to favour rapid development (Ricklefs 1993). Williams (1966) suggested that the length of development might vary because of variation in age-specific mortality, and a number of studies have found that species with high juvenile predation rates have more rapid development (Lack 1968; Case 1978; Crowl & Covich 1990; Promislow & Harvey 1990; Bosque & Bosque 1995; Martin 1995, 2002; Remes & Martin 2002). By contrast, Ricklefs (1968, 1982, 1983, 1993) and Ricklefs *et al.* (1998) (see also Werschkul & Jackson 1979) argued that nest predation is not related to developmental rate in birds and that competition among siblings instead is the primary agent of selection on developmental rate: greater sibling competition favours faster prenatal development because earlier hatching can provide a competitive advantage over siblings.

Although many studies in a variety of taxa support a role for mortality in the evolution of developmental rate (see above), an influence of mortality does not necessarily negate a potential role of other factors, such as sibling competition. Indeed, Royle *et al.* (1999) showed that post-natal growth rates of birds were positively related to rates of extra-pair paternity, which should influence sibling competition. However, prenatal and postnatal developmental rates are genetically independent of one another (Siegel *et al.* 1968; Ricklefs 1984, 1987; *contra* Lack 1968)

and therefore the potential influence of sibling competition on prenatal development remains unclear. Avian prenatal development (incubation) should be an ideal period in which to look for a role of sibling competition because nestling survival hinges upon position in the hatching order in many species; when brood reduction occurs, the last hatched nestling is almost invariably the victim (Mock *et al.* 1990; Stoleson & Beissinger 1995). Thus, sibling competition should strongly favour shorter incubation periods (Ricklefs 1993).

Here, we use comparative analyses of 70 species of bird to test the potential effect of sibling competition on prenatal developmental period. First, we use a kin-selection approach and compare the lengths of incubation across species in which siblings are expected to differ in their average genetic relatedness. Theory predicts that the cost of competition to inclusive fitness decreases as the average relatedness of the interacting individuals decreases, and therefore competition among siblings is expected to be more intense when relatedness is low (Hamilton 1964). Briskie *et al.* (1994) provide empirical support for the connection between competition and relatedness, showing that begging intensity of nestling birds, a measure of sibling competition, increases as the average genetic relatedness of nest-mates declines. Thus, we predict that the length of incubation will be negatively correlated with relatedness if sibling competition is important. We use two indices of average relatedness: the proportion of broods sired by multiple males (extra-pair paternity) and the proportion of broods containing parasitic young (e.g. the result of conspecific or heterospecific females laying eggs in nests of other females).

We also examine the importance of sibling competition by testing for a relationship between the length of incubation and the degree to which offspring hatch asynchronously. Ricklefs (1993) suggested that parents create asynchronous hatching patterns to minimize sibling com-

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petition and thereby allow longer incubation periods, which presumably enhance fitness. According to this hypothesis, sibling competition is determined by parental control of offspring hierarchies based on hatching order. Thus, we also test Ricklefs' (1993) hypothesis that the length of incubation increases with increased hatching asynchrony.

## 2. METHODS

We gathered published data on length of incubation, extra-pair paternity, brood parasitism and hatching asynchrony for as many bird species as we could find in the literature, resulting in a total of 70 species (see electronic Appendix A available on The Royal Society's Publications Web site). We also collected data on two potentially confounding variables: egg size and egg predation. We considered only species with a modal clutch size of greater than one, as individuals in species laying a single egg per clutch will not experience intrabrood sibling competition. In no case were estimates for all variables available from the same population. When estimates of a variable were available from multiple populations we used the unweighted mean in analyses.

Most studies of avian parentage report the percentage of nestlings in a population that are the product of extra-pair fertilizations, but for this analysis the relevant variable is the likelihood that an individual will be raised among nest-mates that are less than full siblings. Thus, using the extensive summaries of avian paternity rates in Schwagmeyer *et al.* (1999) and Møller & Cuervo (2000) as a starting point, we gathered published data on the percentage of broods containing extra-pair young (e.g. young sired by a male other than the social mate of the female). Three of the species included in this analysis have social systems in which multiple males and females form stable breeding groups, and for these species estimates of extra-pair paternity will overestimate the average relatedness among siblings within a nest. Thus, for polygynandrous species (*Calcarius pictus*, *Prunella* spp.), we considered the percentage of multiply sired broods rather than the percentage of extra-pair broods. However, for the sake of brevity we refer to this variable as 'extra-pair paternity' throughout the text. We excluded estimates of parentage that came from electrophoretic analyses unless the authors corrected estimates as in Westneat *et al.* (1987), and thus most of the paternity data reported here comes from DNA fingerprinting studies.

Brood parasitism, in which conspecific or heterospecific females lay their eggs in the nests of other females, may also favour rapid prenatal development. In fact, because in most cases parasitic nestlings are completely unrelated to their nest-mates, brood parasitism should exert even stronger selection on incubation periods. To test the possible importance of variation in parasitism rates across species, we included interspecific and intraspecific parasitism rates as a single variable in all analyses. We did not separate the two rates because, for the species included in this analysis, species that had significant intraspecific parasitism were not reported to be susceptible to interspecific parasitism (e.g. *Progne subis*). Significant and systematic intraspecific brood parasitism was also relatively rare in the species included in this analysis, and thus most estimates of brood parasitism reflect interspecific parasitism by brown-headed cowbirds (*Molothrus ater*) and common cuckoos (*Cuculus canorus*). None of the species in this analysis from the orders Galliformes, Anseriformes, Strigiformes and Ciconiiformes are known to be hosts

for obligate interspecific brood parasites (although some are subject to intraspecific parasitism), and thus when no mention could be found of brood parasitism (either in general species accounts or in the parasitism reviews of Friedmann *et al.* (1977) and Davies (2000)), we assumed that parasitism is infrequent and assigned a zero value for the species. Species known to be susceptible to parasitism (e.g. from general species accounts; most Passeriformes), but for which no estimate was available, were excluded from analysis.

Hatching asynchrony, if it results in dominance hierarchies that cannot be overcome by individual selection for more rapid development, may eliminate sibling competition. We considered three levels of asynchrony: synchronous (all young hatch within 24 h of one another), partially asynchronous (hatching interval between first and last young is greater than 24 h, but not completely asynchronous) and asynchronous (one young hatches per day). We chose to use three categories rather than a synchronous-asynchronous dichotomy because many species in our sample were neither completely synchronous nor asynchronous (see also Clark & Wilson 1981). Even a three-tier categorical approach may obscure some meaningful variation, but insufficient data are available to consider asynchrony as a continuous variable.

Incubation period has a strong positive relationship with egg size (e.g. Worth 1940; Rahn & Ar 1974). Thus, to control for this allometric effect, we included egg volume (calculated as in Ricklefs 1993) as an independent variable in all analyses.

For most bird species, nest predation is the primary source of mortality for eggs (Ricklefs 1969; Martin 1992) and may favour shorter incubation periods (Lack 1968; Bosque & Bosque 1995; Martin 1995, 2002). Thus, we included the percentage of nests lost to predators as an independent variable in our analyses. We assume that interspecific differences in the total number of nests lost to predation reflect similar differences in egg mortality (e.g. Ricklefs 1969). Predation typically results in the loss of all eggs in a nest, so for most species the percentage of nests lost to predators should provide a reasonable index of time-dependent mortality. However, for some of the larger precocial species (e.g. *Chen* spp.), predation apparently rarely results in the loss of the entire nest, and for these species rates of total nest loss will underestimate mortality of individual eggs. Thus, when partial predation of nests was reported to be frequent, we used the percentage of eggs lost to predators as an estimate of time-dependent mortality.

Although a correlation exists between the developmental stage of the neonate and the length of incubation (e.g. Boersma 1982; Ricklefs 1984), we did not include developmental mode as a predictor because this correlation is caused by allometric effects of egg size rather than by a difference between altricial and precocial young in developmental rate (Ricklefs & Starck 1998). Nonetheless, to be certain, we tested and confirmed the lack of a relationship between the precocity of the neonate and the length of incubation in our sample ( $p = 0.62$ ) and thus we do not consider developmental mode further.

To control for possible phylogenetic effects, we analysed independent contrasts (Felsenstein 1985) generated by the CRUNCH option of the program CAIC (Purvis & Rambaut 1995). We also present results of analyses on uncorrected species means. We generally followed the phylogeny of Sibley & Ahlquist (1990) to infer evolutionary relationships among the species in this analysis, but included more recent information from Sheldon *et al.* (1992) for the genera *Parus* and *Poecile*, Sheldon & Winkler (1993) for the subfamily Hirundinidae, Patten & Fugate (1998) for the New World sparrows and buntings in Emberizidae, and

Ohta *et al.* (2000) for *Panurus biarmicus* to increase the resolution of the phylogeny. The phylogeny used in this analysis is available from the authors upon request.

We evaluated two models for determining the length of branches in the phylogeny, which are used to standardize the independent contrasts: a punctuational model of evolution in which all branches are of equal length, and the method suggested by Grafen (1989) in which the length of a branch is proportional to the number of taxa it supports. The punctuational model produced contrasts that met the assumptions of the statistical model (Purvis & Rambaut 1995), whereas Grafen's approach did not, and therefore we present only the results obtained from contrasts generated assuming equal branch lengths.

For all analyses, we used a regression approach to examine the relationship between sibling competition and incubation length. We forced all independent variables into the model to analyse the effect of sibling competition on the length of incubation independent of any effect of egg size or nest predation. Following Harvey & Pagel (1991), the regression on independent contrasts was forced through the origin. All variables were transformed prior to analysis to achieve normality: egg size and incubation period were log-transformed, and extra-pair paternity, predation rate and brood parasitism were arcsin-transformed. The residuals from all regressions were normally distributed.

### 3. RESULTS

Analysis of species means showed that length of incubation increased strongly with egg size ( $b = 0.763$ ,  $p < 0.001$ ), but was not related to nest predation ( $b = -0.015$ ,  $p = 0.786$ ). Length of incubation was negatively related to extra-pair paternity after controlling for the effect of the other independent variables (figure 1a;  $n = 70$ ,  $b = -0.178$ ,  $p = 0.007$ ). Brood parasitism was also negatively related to the length of incubation (figure 1b;  $b = -0.119$ ,  $p = 0.04$ ), whereas hatching asynchrony was positively related to the length of incubation (figure 1c;  $b = 0.095$ ,  $p = 0.021$ ).

The pattern that emerged from the analysis of independent contrasts was somewhat different. The length of incubation was still negatively related to extra-pair paternity (figure 2a;  $n = 67$ ,  $b = -0.239$ ,  $p = 0.029$ ) and positively related to egg volume ( $b = 0.474$ ,  $p < 0.001$ ). However, after controlling for phylogeny, neither brood parasitism (figure 2b;  $b = -0.051$ ,  $p = 0.643$ ) nor hatching asynchrony (figure 2c;  $b = 0.125$ ,  $p = 0.248$ ) was significantly associated with length of incubation. Nest predation ( $b = 0.155$ ,  $p = 0.156$ ) remained insignificant in explaining variation in the length of incubation.

The results of the comparative analyses can be influenced by the taxonomic scale of the study, even if phylogeny is controlled for with independent contrasts. To test the consistency of our results, we repeated our analysis on the raw data for species in the order Passeriformes, the best-represented group in our dataset. Within this subset of data, only extra-pair paternity was significantly related to length of incubation ( $n = 46$ ,  $b = -0.386$ ,  $p = 0.007$ ). Egg volume, which explains a significant part of the variation in the length of incubation across orders, was only marginally related to the length of incubation among passerines ( $b = 0.248$ ,  $p = 0.077$ ). Brood parasitism

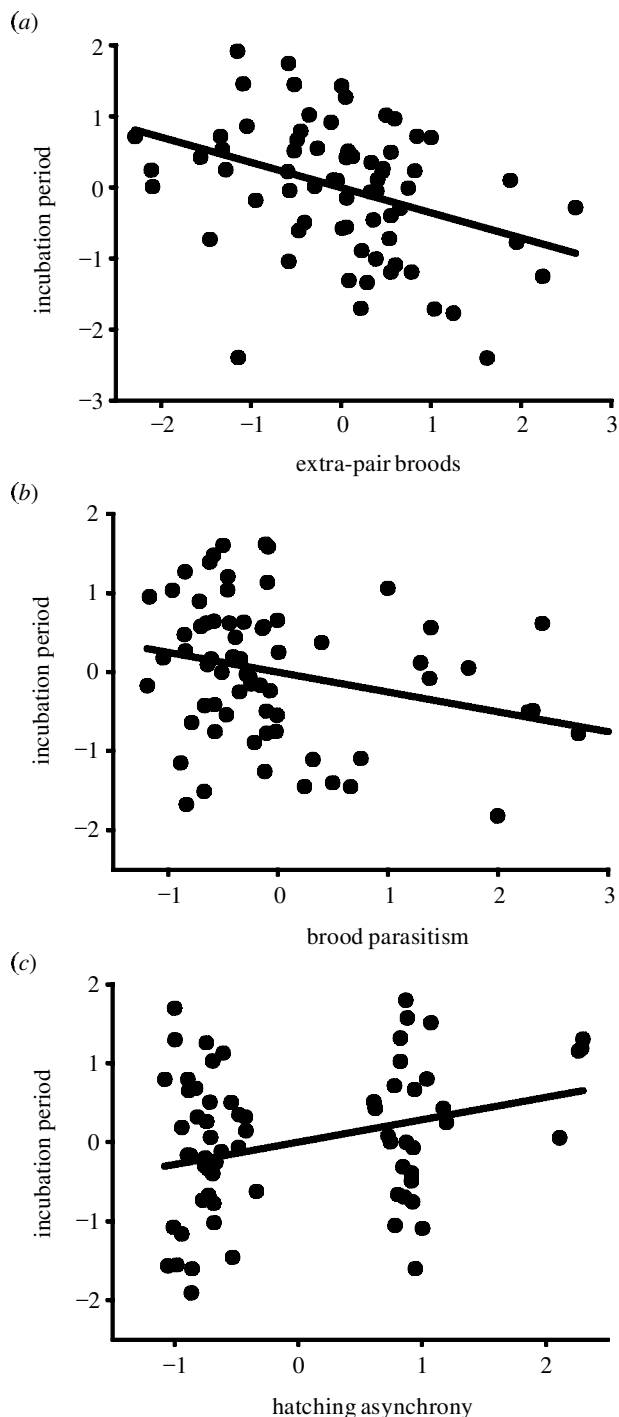


Figure 1. Partial regression plots of residual values showing interspecific variation ( $n = 70$  species) in the incubation period relative to (a) extra-pair paternity, (b) brood parasitism and (c) degree of hatching asynchrony after controlling for the effect of other independent variables in a multiple regression. (a) The incubation period is shorter in species with high rates of extra-pair paternity ( $b = -0.178$ ,  $p = 0.007$ ); (b) the incubation period is shorter in species with high rates of brood parasitism ( $b = -0.119$ ,  $p = 0.04$ ); and (c) the incubation period is positively associated with the degree of hatching asynchrony ( $b = 0.095$ ,  $p = 0.021$ ).

( $b = -0.103$ ,  $p = 0.461$ ), hatching asynchrony ( $b = 0.162$ ,  $p = 0.243$ ) and predation ( $b = -0.192$ ,  $p = 0.164$ ) did not explain the variation in incubation period.

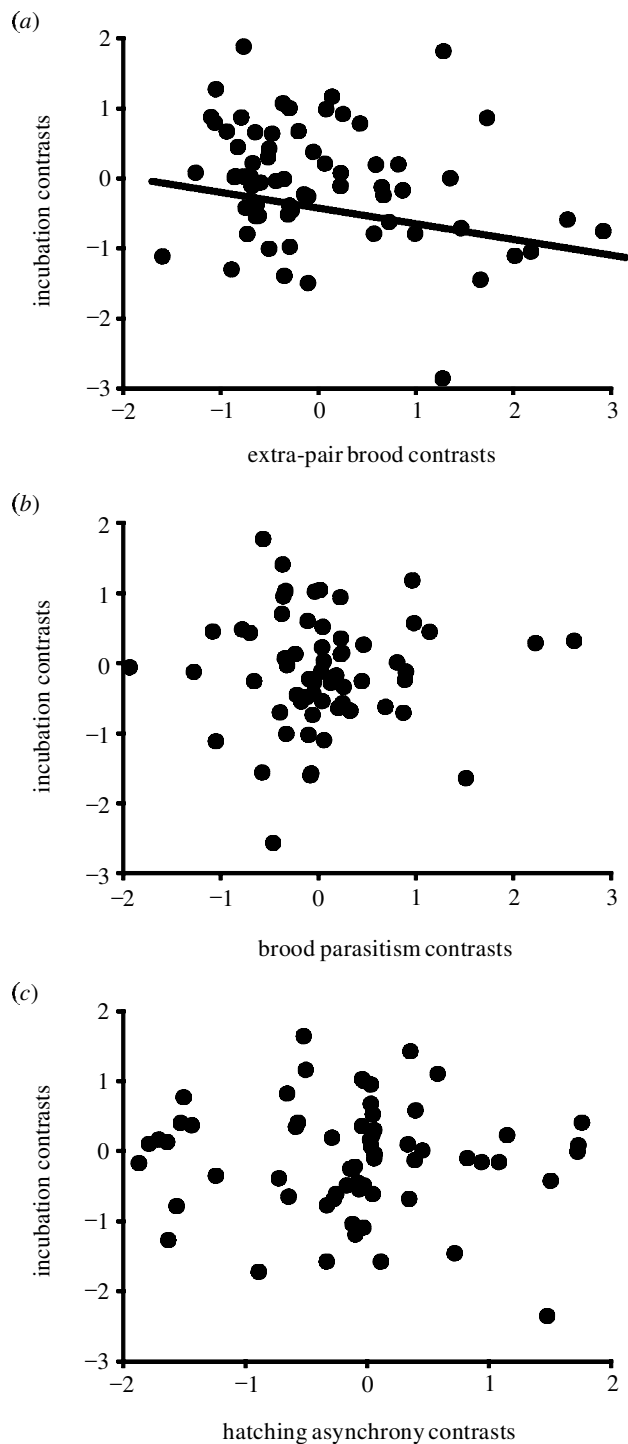


Figure 2. Partial regression plots of residuals of phylogenetically independent contrasts ( $n = 67$  contrasts) in the incubation period relative to residuals of contrasts in (a) extra-pair paternity, (b) brood parasitism, and (c) degree of hatching asynchrony. Residuals produced by multiple regression including all independent variables. (a) The incubation period decreases with increasing extra-pair paternity ( $b = -0.239$ ,  $p = 0.029$ ). There is no relationship between incubation contrasts and (b) brood parasitism contrasts ( $b = -0.051$ ,  $p = 0.643$ ) or (c) hatching asynchrony contrasts ( $b = 0.125$ ,  $p = 0.248$ ).

#### 4. DISCUSSION

Based largely on theoretical considerations, sibling competition has been proposed as a key evolutionary pressure

driving interspecific variation in developmental rates (Ricklefs 1982, 1993; Ricklefs & Starck 1998). Testing this hypothesis depends on quantifying variation in sibling competition. Variation in the genetic relatedness of siblings seems one reasonable way to estimate variation in sibling competition; as the average relatedness among nest-mates decreases, siblings can afford to compete more fiercely because the cost to inclusive fitness decreases, and the benefits of developing faster can be large when it yields a higher position in the dominance hierarchy. We used two measures that should reflect broad differences between species in the average relatedness of nest-mates: extra-pair paternity and brood parasitism. Royle *et al.* (1999) showed that postnatal growth rates of birds were correlated with rates of extra-pair paternity. We show here that extra-pair paternity, as a proxy for sibling competition, is also related to more rapid prenatal development.

The effect of brood parasitism was mixed. Based on the analysis of the raw data, our results suggested that brood parasitism may exert some influence on the length of incubation, but the effect was not significant after controlling for phylogeny nor was it significant when considering only Passeriformes. The lack of relationship within Passeriformes suggests caution is needed in interpreting the significant relationship in the complete set of raw data; this relationship must depend in part upon differences between higher-level taxa, which may not reflect sibling competition. Nonetheless, given the consistently strong relationship between extra-pair paternity and length of incubation, it is somewhat surprising that no effect of brood parasitism was evident, especially when analysis was restricted to passerines. Based on our kin-selection approach, the effect of brood parasitism on developmental rate should be stronger than that of extra-pair paternity because, in general, brood parasitism results in the introduction of genetically unrelated individuals into a nest. Thus, the inclusive fitness costs that are presumed to restrain competition among siblings are absent. However, estimates of brood parasitism vary extensively across populations of a single species, such that determination of the level of selection pressure on a species over its range and over evolutionary time may be difficult. This problem is compounded by the fact that much variation in parasitism may arise from recent changes in habitat that have either allowed brood parasites to expand their range and exploit new hosts or made old hosts more susceptible.

Our third measure of sibling competition followed Ricklefs (1993), who proposed that parents create asynchronous hatching patterns in their offspring to blunt the selective force of sibling competition and allow longer incubation periods. Hatching asynchrony was indeed positively related to incubation period in the raw data, but not among the independent contrasts. Moreover, hatching asynchrony was not significant in the analysis restricted to Passeriformes. This suggests that the significant relationship seen in the complete set of raw data is a result of differences between higher-level taxa. Thus, within our sample, hatching asynchrony seems relatively unimportant in explaining variation in incubation period.

Nest predation is expected to favour more rapid embryonic development (Lack 1968; Ricklefs 1993; Bosque & Bosque 1995). We found that nest predation did not explain variation in incubation period in our sample. Sev-

eral factors may have confounded our analyses, however. First, some of the estimates of nest predation are based on small samples gathered over a short period of time. Second, the estimates of nest predation used in this study may reflect current ecological conditions that differ from those present over evolutionary time because of changes in habitat quality or the abundance and composition of the predator community. Finally, when comparisons are made across geographical regions, or between distantly related species, the relationship between predation and length of incubation becomes more difficult to isolate (Ricklefs 1993; Martin *et al.* 2000; Martin 2002). Nonetheless, we find no evidence for a role of nest predation in determining lengths of the incubation periods of the species examined here.

Ultimately, all three of our measures of sibling competition were related to length of the incubation period in the predicted directions, although two of the measures (brood parasitism and hatching asynchrony) showed no relationship once phylogenetic effects were removed. On the one hand, that all three measures showed relationships in the directions predicted by sibling competition provides some support for this hypothesis. On the other hand, the weak and mixed nature of the results for two of the measures raises questions. The relationship between the incubation period and extra-pair paternity was strongest and clearest, and may reflect effects of sibling competition. However, rather than being a cause-and-effect relationship, the relationship between extra-pair paternity and the length of incubation may arise indirectly from correlated selection on both traits.

Variation in extrinsic mortality can drive the evolution of life-history strategies (e.g. Gadgil & Bossert 1970; Michod 1979; Reznick 1982; Reznick *et al.* 1990), and longer incubation periods are associated with low adult mortality (Ricklefs 1993; Martin 2002). Extra-pair mating is a form of investment in current reproduction and may thus also be influenced by adult mortality, especially if garnering extra-pair copulations incurs a cost to future survival or reproduction (e.g. Westneat & Rambo 2000 (see also Wink & Dyrce 1999)). Consequently, incubation period and extra-pair paternity may be correlated as an indirect consequence of adult mortality acting on both traits, rather than representing the effect of sibling competition. Thus, the importance of sibling competition in determining incubation period remains unclear, although our results suggest that it may play a role. At the same time, the strength of correlations observed here between extra-pair paternity and length of incubation suggest at the very least that life-history strategies represent linkages among a larger suite of traits than previously recognized and argue for a broad approach to considerations of the evolution of life histories.

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