Predictably Philandering Females Prompt
Poor Paternal Provisioning

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ABSTRACT: One predicted cost of female infidelity in socially monogamous species is that cuckolded males should provide less parental care. This relationship is robust across species, but evidence is ambiguous within species. We do not know whether individual males reduce their care when paired with cheating females compared with when paired with faithful females (within-male adjustment) or, alternatively, if the males that pair with cheating females are the same males that provide less parental care in general (between-male effect). Our exceptionally extensive long-term data set of repeated observations of a wild passerine allows us to disentangle paternal care adjustment within males—within pairs and between males—while accounting for environmental variables. We found a within-male adjustment of paternal provisioning, but not incubation effort, relative to the cuckoldry in their nest. This effect was mainly driven by females differing consistently in their fidelity. There was no evidence that this within-male adjustment also took place across broods with the same female, and we found no between-male effect. Interestingly, males that gained more extrapair paternity provided less care. Data from a cross-foster experiment suggested that males did not use kin recognition to assess paternity. Our results provide insight into the role of individual variation in parental care and mating systems.

Keywords: parental investment, extrapair paternity, social feedback, monogamy, mating systems.

Introduction

The question of why females are unfaithful in socially monogamous species is currently the subject of a vibrant debate (Forstmeier et al. 2014; Arct et al. 2015; Drobniak et al.

2015; Forstmeier 2015; Griffith 2015; Nakagawa et al. 2015; Reid 2015). The theoretical predictions for female infidelity are clear: females are expected to gain indirect fitness benefits through higher genetic quality of the extrapair male, better genetic compatibility with the extrapair male in comparison to the social mate, or fertility insurance (Griffith et al. 2002; Akçay and Roughgarden 2007). Extrapair matings are thus expected to help to avoid inbreeding, improve genetic diversity and immunocompetence, and ensure gamete fertilization, all of which should enhance the fitness of the female and her offspring (Griffith et al. 2002). Despite these theories, the empirical evidence for indirect benefits is conflicting (e.g., Møller and Alatalo 1999; Arnqvist and Kirkpatrick 2005; Rosivall et al. 2009; Hsu et al. 2014; Bowers et al. 2015). Meta-analyses have also provided conflicting results for whether females gain fitness benefits from having extrapair offspring (EPO; Akçay and Roughgarden 2007; Arct et al. 2015) and even suggest that female infidelity is costly (Hsu et al. 2015). To further our understanding of the evolution of female polygamy, it is crucial to understand not only the benefits but also the costs of females producing EPO (Nakagawa et al. 2015). One such cost could be reduced parental care by the cuckolded male (Burke et al. 1989). For example, in male reed buntings (*Emberiza schoeniclus*), provisioning was positively correlated with paternity in his brood (Dixon et al. 1994).

Parental investment is defined as costly behavior by adults that increases the survival chances of the young (Trivers 1972; Royle et al. 2012). It follows that animals should invest in costly parenting only if the fitness benefits outweigh the costs. Thus, a parent's optimal investment is expected to be defined by the benefits for the offspring and the genetic relatedness between the parent and offspring (Hamilton 1964). Different theories make distinct predictions about how males should optimize their care according to the number of EPO in their current brood. Depending on the life history and

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ecology of the species, reduced care, no adjustment, or even increased paternal care have all been predicted as reactions to a change in the number of EPO (Kempenaers and Sheldon 1997; Whittingham and Dunn 2001; Holen and Johnstone 2007). The favored theory of how males should optimize their parental investment with respect to being cuckolded is that they should provide less care to a brood that contains more EPO than to a brood of the same female that contains no or fewer EPO—the paternal care adjustment hypothesis.

When females produce EPO (for a review, see Kempenaers and Schlicht 2010), males cannot know for certain that all the offspring he cares for are genetically related to him (certainty of paternity), unless he guards her completely during her fertile period (Birkhead and Møller 1998). Therefore, when paternity is less certain and other mating opportunities exist, males should invest less into parental care (Maynard-Smith 1977; Grafen 1980). There is ample empirical evidence for such a negative relationship across species between male care (paternal care in the following) and the mating system (Griffin et al. 2013). However, it is unclear whether individual males actively adjust their paternal investment according to the number of EPOs present in the brood to which they are providing care. Many empirical data have been gathered to solidify the paternal care–paternity relationship in species ranging from insects to mammals, but these studies have resulted in negative, positive, and no relationships (for a review and meta-analysis, see Alonzo 2010 and Griffin et al. 2013, respectively). One reason for this might be that such correlations can arise from two biologically distinct mechanisms. First, males might adjust their paternal care directly according to how faithful their partner is (within-male adjustment hypothesis). Second, males may differ consistently in how much parental care they provide, and in turn, these males might pair nonrandomly with females that differ consistently in how faithful they are. This is repeatable phenotypic variation with assortative mating, or the between-male effect hypothesis. In this case, the association between paternal care and female fidelity might be the result of a noncausal mechanism of assortative mating for quality. Distinguishing between these two hypotheses would be informative about whether females pay for infidelity with reduced paternal care and further our understanding of the evolution of mating systems and parental investment. Notably, if the between-male effect hypothesis is supported, then this would reduce the argument for infidelity being costly to females and therefore also reduce the need to identify a counteracting female benefit (Griffith et al. 2002; Akçay and Roughgarden 2007; see also Forstmeier 2014; Hsu 2015; Nakagawa et al. 2015).

For the within-male adjustment hypothesis to hold, the assumption has to be made that males can assess and respond to the paternity of their chicks (Burke et al. 1989). Such a flexible adjustment requires the detection of small changes in the probability of paternity, and the adjustment might be suboptimal, especially if the assessment of cuckoldry is imperfect and based on cues other than a male's genetic relatedness to individual offspring (e.g., Burke et al. 1989; Davies et al. 1992). The ability of fathers to identify their own offspring, while intriguing, has received very little empirical support. Some birds, at least, have a sense of smell (Steiger et al. 2008), and it may be possible that birds can use this sense to discern kinship or genetic similarity (Bonadonna and Sanz-Aguilar 2012; Krause et al. 2012). The general consensus, however, is that parents are unable to assess relatedness directly by any mechanism (Amo et al. 2014). Furthermore, even if birds can assess relatedness, it has been suggested that this is unlikely to be precise enough to adjust paternal care to the optimal level (Kempenaers and Sheldon 1996; Krause et al. 2012). A likely and more gradated cue for a male to assess his degree of paternity certainty is the behavior of his female during her fertile period, for example, deviations in her pattern of presence or absence (Kempenaers and Sheldon 1996). Furthermore, the assumption that males can estimate and respond to their paternity fails to consider the cost to males of assessing their paternity and the potentially high risk of making wrong allocation decisions. Therefore, to account for such costs, we predict that males should follow a simple reaction norm to environmental cues correlated with paternity—or to cues from the partner—that suffice in guiding optimal parental care allocation decisions for both sexes.

Below we (1) briefly reiterate the difficulty of testing the paternal care adjustment hypotheses in observational data and provide solutions for detailed hypotheses on how the pattern can come about (Kempenaers and Sheldon 1996, 1997, 1998; Sheldon 2002). We then (2) provide a case study in which we apply mixed models to revisit the relationship between paternal care and paternity in a long-term data set that is exceptionally well suited to distinguishing between the hypotheses for paternal care adjustment.

The Problem

Any pattern found between paternal care and paternity in raw data will not necessarily be informative about the biological processes at play. The main reason for this is that any trade-off happens at an individual level (within-individual process; Stearns 1992), which needs to be analytically distinguished from any between-individual process (fig. 1A–1C). Three hypotheses other than the within-male adjustment and between-male effect hypotheses could also explain an association among or within males between paternal care and paternity share in the brood: differences in state within individual males, effects of the partner within individual males, and environmental effects. We explain these briefly below.
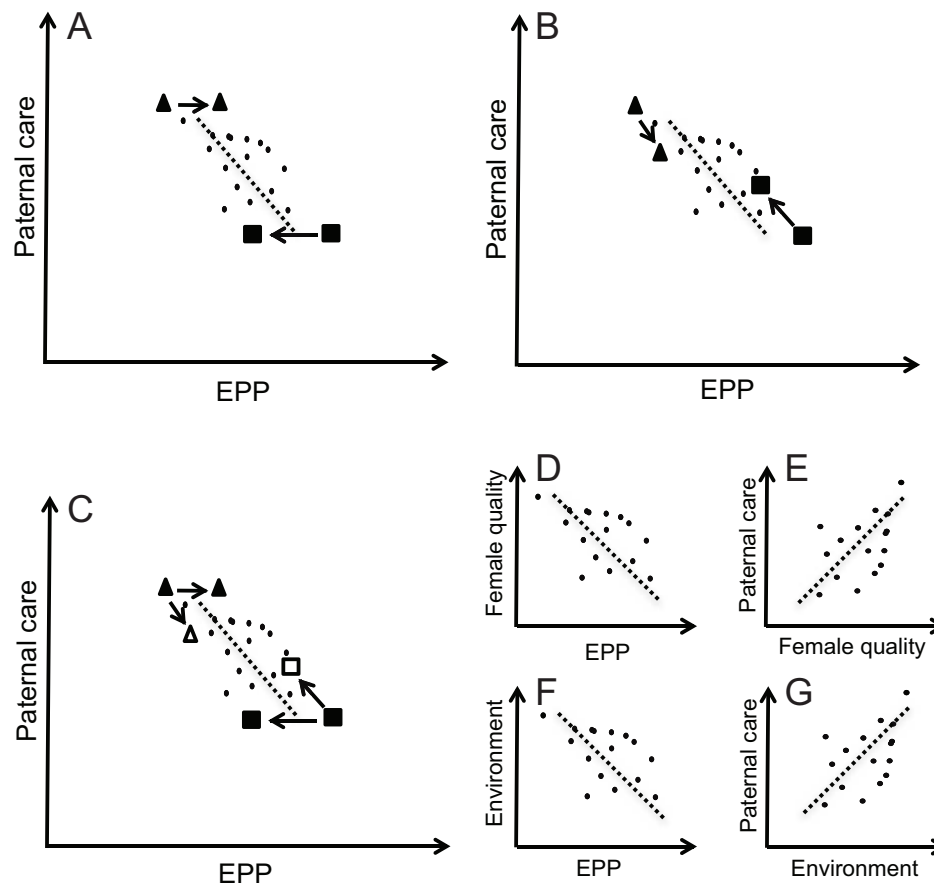
Figure 1: Schematic representation of the different possible associations between paternal care and extrapair paternity (EPP). Squares and triangles denote individual males. *A*, Between-male effects: males that are paired with females that produce broods with higher levels of EPP are the same males that provide little parental care, and vice versa. Paternal care does not change in relation to a change in EPP within the same pair for the between-individual effect to persist. *B*, Within-male adjustment: individual males adjust their care directly in response to the EPP in successive broods. *C*, Within-male but between-pair adjustment: males do not adjust paternal care to changes in EPP in subsequent broods with the same female partner (filled symbols), but males do adjust their paternal care when they pair with a different female who produces a brood with a different degree of EPP (open symbols reflect new partners). *D–G*, An apparent association between paternal care and EPP can result from two independent associations between (1) female individual quality and extrapair paternity (*D*) or paternal care (*E*) or between (2) environmental effects and EPP (*F*) or paternal care (*G*).

Male State. There is within-male variation in flexible traits, such as condition, health, experience, or traits that change with age (Houston and McNamara 2002). Age, especially, can covary with the quality of the female partner that a male can secure, with the level of extrapair paternity (EPP) in the brood, and, potentially, with the quality of paternal care. For example, inexperienced males may be poorer at mate guarding and be time constrained (Schwagmeyer et al. 2012). Thus, the female paired with such a male may gain EPOs while, simultaneously, the male may not provide a high level of paternal care. Extrapair sires are predominantly older males (Wetton et al. 1991; Cleasby and Nakagawa 2012; Hsu et al. 2015), which could mean that correlated differences in parental investment between males with and

without EPP could indirectly be driven by male age. Several studies have shown that older males are better at obtaining EPPs and also invest more into paternal care than younger males (Kempenaers and Sheldon 1997; Houston and Mc-Namara 2002; Velando et al. 2006; Hammers et al. 2012). Thus, age alone as a flexible male state might potentially drive any association between paternal care and paternity. To test for this mechanism, one needs to analyze longitudinal data with repeated measures for within-male patterns, accounting for age.

Effects of the Partner. Males might adjust their contribution to care according to the individual quality of their partnered female (differential allocation hypothesis; Shel-

don 2000; Pilastro et al. 2003; Matessi et al. 2009; Morales et al. 2009). If females differ consistently in the number of EPO in their broods, and the quantity of EPO is associated with individual quality (Forstmeier et al. 2011), then a misleading association with paternal care can result (fig. 1*D*). A male paired up with a low-quality female might be less likely to invest into the brood (fig. 1*E*) and instead use their resources in seeking opportunities to gain EPP elsewhere (Kokko and Jennions 2008). Current condition and thus the value of the female to the male may be phenotypically flexible and signaled by, for instance, her age, health status, or another trait. Any such effect might cause an apparent association between paternal care and EPP (Alonzo 2010). Males might, however, keep their level of care constant within a pair but not when changing partners (fig. 1*C*), because such consistent behavior might encourage mate retention and thus increase a male's chances of future reproductive success (Sheldon 2000; Servedio et al. 2013). Such a system, where males decide about their investment and stick with their decision throughout the reproductive bout or pair bond, is termed a sealed bid (Houston et al. 2005). To test whether individual males adjust their allocation of resources in repeated breeding attempts between different partners or within the same partner, depending on the individual quality and state of their partner, one needs repeated measures of males paired with different females.

Environmental Variables. Environmental stochasticity may affect both EPP and paternal care through, for instance, food availability (Schwagmeyer et al. 2012). Changes in environmental variables across a season might lead to an apparent association of EPP with paternal care (fig. 1*F*, 1*G*) across successive broods (Kempenaers and Sheldon 1997).

The need for a study that can distinguish these hypotheses was highlighted nearly 2 decades ago (Kempenaers and Sheldon 1997; Sheldon 2002). We can only start to reveal the actual costs of infidelity for females and better understand the evolution of mating systems, monogamy, and parental care once we know whether within-male adjustment relative to EPP is a biological reality (Griffin et al. 2013). Only experimentally induced EPP would allow us to test directly the parental care adjustment hypothesis and to assess the costs of female infidelity. Such experiments are difficult to achieve because their design is inherently limited to those cues that males can detect and use to make allocation decisions. Therefore, such experiments could be severely confounded. Without prior knowledge about correlational relationships, it is unclear if and how experiments for causation between paternal care and paternity should be conducted.

Analyzing patterns in repeated measures can achieve a better understanding of the associations between paternity and paternal care within and between males. To test for within-male adjustment, one needs repeated measures of the same males in broods that contain different levels of EPO (Dixon et al. 1994). The published studies with such a design are surprisingly scarce and have very small sample sizes with repeated measures, ranging from $N = 5$ (Williams and Hale 2008) to a maximum of $N = 27$ (Westneat 2001). A correlational approach with high statistical power—and that handles the caveats discussed above—is therefore timely.

Case Study

Here, we test the paternal care adjustment hypothesis, using a data set from house sparrows (*Passer domesticus*). Paternal care in house sparrows is linked with direct fitness benefits: chicks that receive more paternal care from their social father have a higher annual and lifetime fitness (Schroeder et al. 2013). Thus, even a partial reduction in paternal care would likely incur fitness costs to female sparrows. Our data set contains repeated measures of parental care from 200 males. House sparrows breed multiple times a year and often change social partners. For the first time, this data set allows us to disentangle within-male paternal care adjustment from between-male effects, while accounting for environmental variables. We then continue to distinguish whether the within-male adjustment takes place within or between pairs.

Material and Methods

Paternal Care Data

We used data from a natural house sparrow population breeding on Lundy Island (51°10′N, 4°40′W; Cleasby et al. 2011). When captured, birds were marked with a metal ring from the British Trust for Ornithology and an individual color ring combination. We also equipped birds with passive-integrated transponders (Schroeder et al. 2011*b*). We identified individuals attending a nest box by their unique color ring combination, by direct observations, or by video recordings made specifically for this purpose (Nakagawa et al. 2007; Schroeder et al. 2013). We also identified parents with nest box antennae, permanently installed on some nest boxes, that detect the presence and unique identification (ID) of the passive-integrated transponder of a bird when it enters the nest box (Schroeder et al. 2011*b*). We used data on two measures of parental care—incubation and provisioning behavior—from the years 2004–2012. We placed video cameras on the ground in front of the nest boxes, such that the field of view included a 30-cm radius around the nest box, and recorded for 90 min (Nakagawa et al. 2007). The numbers of eggs and chicks were counted. We used only that part of the video from the moment

when the first bird returned to the nest, in order to avoid latency artifacts from birds being scared of the camera (Nakagawa et al. 2007). This resulted in most videos being slightly shorter than 90 min (mean recording time ± SD: incubation: 88.3 ± 7.44 min, $N = 1{,}199$ on 652 broods; nestling provisioning: 88.3 ± 6.53 min, $N = 1{,}430$ on 661 broods; note that the identical values for the mean recording times are a coincidence).

Incubation behavior was scored when a breeding bird had spent at least 1 min in the nest box. We used the time (min h^{-1}) a male spent incubating as a measure of paternal incubation care. Provisioning behavior was scored when a bird either entered the nest box in which there were chicks present or fed chicks from outside the nest box. We used the number of visits (visits h^{-1}) of a male to his nest box as a measure of paternal care in the form of nestling provisioning. For more details on methods of parental care data collection, see Nakagawa et al. (2007) and Schroeder et al. (2013). Provisioning observations took place on broods that were cross-fostered at day 2 after hatching ($N = 937$ observations on 416 broods) and on broods that did not experience any cross-fostering treatment ($N = 493$ observations on 245 broods). Data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.0t313 (Schroeder et al. 2016).

Extrapair Paternity

We sampled DNA from nearly every fledged sparrow caught on Lundy, which we then genotyped at 13 polymorphic microsatellite loci (Schroeder et al. 2011a; Hsu et al. 2015). The usefulness of these loci for parentage analysis is documented elsewhere (Dawson et al. 2012). With these data, we determined the genetic ancestry of every genotyped bird and calculated the number of EPO in each brood (Hsu et al. 2014). We then calculated the ratio of EPO to all genotyped offspring from each original brood. Typically, in each year, 99% of chicks that survived past the age of 2 days were genotyped and assigned paternity (Schroeder et al. 2011a). Overall, from 2000 to 2012, we assigned paternity to more than 96% of chicks that were alive as hatchlings (Hsu et al. 2015).

Statistical Analyses

First, we tested whether there was variation in EPO among and within males, females, and pairs by calculating the repeatability of the proportion of EPO among males (male ID), among females (female ID), and among unique parent-pairs (pair ID). The repeatability is a measure of the proportion of variance in a trait explained by within-subject consistency and between-subject variation. We modeled the number of EPO and WPO in a generalized linear mixed

model (GLMM) with no fixed effects and with male ID in a first model, pair ID in a second model, and female ID in a third model as the respective single random effect on the intercept:

$$p_{ij} = \text{logit}^{-1}(1 + \alpha_i + \varepsilon_{ij}), \tag{1}$$

where p_{ij} is the underlying (latent) probability of being an EPO for the ith chick of the jth male (or, in the second analysis, pair). The intercept is set to one on the link scale, α_i is the random effect (i.e., male ID, pair ID, or female ID) with a variance of σ_α^2, and ε_{ij} is the residual (additive overdispersion) term on the link scale with a variance of σ_ε^2. We calculated the link-scale repeatability, following Nakagawa and Schielzeth (2010), as

$$R_L = \frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_\varepsilon^2 + (\pi^2/3)}. \tag{2}$$

Within-Male Adjustment versus Between-Male Effect. We tested for within-male adjustment for whether a male provided less care to a brood containing more EPO than one with fewer EPO. We used within-subject centering, using GLMMs (van de Pol and Wright 2009). For both incubation and nestling visits, we modeled the identity of the male (male ID) as a random intercept, which accounts for between-male variance (differences between males). We then used two fixed predictors: one to estimate the within-male adjustment (within-male adjustment) to being cuckolded (W_m) and one for the between-male (B_m) effect of being cuckolded. To estimate W_m, we subtracted the average frequency of EPO for the focal male (between-male effect; B_m) from each individual observation of the focal male:

$$W_m = x_{ijk} - \bar{x}_j, \tag{3}$$

$$B_m = \bar{x}_j, \tag{4}$$

where x_{ijk} is the ith observation on individual j of pair k.

We modeled both response variables (incubation behavior and provisioning) with the same model structure (W_m and B_m) and added the following fixed and random effects because of their biological relevance: we know that the age of the chicks (chick age), the number of chicks in the brood (clutch size), and the day of the year each affect paternal care, and we therefore center-scaled these and added them to the model as covariates (Westneat et al. 2011). We have shown before that the time of day did not statistically significantly affect the frequency of nestling visits; therefore, we did not add this covariate to the model (Schroeder et al. 2013). We added year and the brood identity (brood ID) as random effects to account for annual stochasticity and pseudoreplication. Incubation time was modeled with Gauss-

ian errors, and nestling visits were modeled as counts (h^{-1}) with a Poisson error distribution.

Effect of the Partner. We found within-male adjustment: males adjust their provisioning behavior—but not incubation behavior—according to the extrapair offspring their partners produced. We subsequently wanted to know whether this within-male adjustment was due to different partners producing different numbers of EPO, due to the same partner producing different numbers of EPO in successive broods with the same male, or both. We constructed another GLMM with provisioning behavior as the response variable. Male birds were nested in pairs, which differed from each other by the different identity of the female partner, adding one hierarchically nested layer to the model (i.e., male ID fitted as a cross-classified random effect within pairs). We used three fixed covariates to model variation within males within pairs (W_{mp}), within males but between pairs (W_mB_p), and between males (B_m; eq. [4]):

$$W_{mp} = (x - \bar{x}_j) - \overline{(x_{ijk} - \bar{x}_j)_k}, \qquad (5)$$

where W_{mp} excludes any between-male variation and tests only for an effect that takes place within pairs and within males;

$$W_mB_p = \overline{(x_{ijk} - \bar{x}_j)_k}, \qquad (6)$$

where W_mB_p excludes between-male variation and tests for an effect between pairs but within males. We also added clutch size and chick age as covariates. In addition to bird ID, year, and brood ID, pair ID was added as a random effect to account for correlated data structures. Subject centering has the potential to be biased, especially if used on small data sets (Phillimore et al. 2010). Our data set is relatively large; however, we tested the robustness of our results by running bivariate GLMMs, which provide unbiased results (Phillimore et al. 2010), in which we assessed the variance-covariance matrices. These models returned qualitatively similar results.

Male State. We tested whether males adjusted their provisioning rate differently over the course of their life span. We used the model described under effect of the partner and added a covariate of male age (age) and an interaction of age with W_mB_p, since W_mB_p was the level on which we found a statistically significant within-male adjustment effect. We also tested for an interaction of a squared effect of male age with W_mB_p to account for nonlinear changes with age. We then tested whether there was an association with the adjustment males made and the number of EPO this male gained in the year (EPO gain). Therefore, we added an interaction of EPO gain with W_mB_p to the model.

Environmental Effects. We then tested whether changes in the environment affected the within-male paternal care adjustments. Males might adjust their behavior according to food availability, which can vary over the course of a season. We therefore added day of the year as a continuous linear predictor and also tested an interaction of day with W_mB_p. We modeled whether the brood order affected paternal care by adding brood number (numbered within pairs consecutively within a year) as a covariate to the model and an interaction of it with W_mB_p. We considered whether a brood was cross-fostered in this analysis, because even although we consider it unlikely, cross-fostering could affect our results if males were able to assess their kinship to the offspring they cared for. We added the two-level factor fostered as an environmental variable to this model and an interaction of it with W_mB_p to test whether the within-male adjustment changed, depending on the degree of kinship with the cared-for offspring. If we were to find an effect here, this analysis could suggest that males may be able to assess and adjust to genetic relatedness to the nest they care for (but see discussion).

We used MCMCglmm (ver. 2.19) in R (ver. 3.10; R Development Core Team 2015) to calculate parameter estimates and 95% credibility intervals (CIs; Hadfield 2010). We considered fixed effects as statistically significant when their 95% CI did not span 0. We mention minimum probability values (MCMC-P) to describe nonsignificant results. These refer to pMCMC as calculated in MCMCglmm, which is twice the MCMC estimate of the probability that the 95% CI does not span 0 and can therefore be interpreted in a similar way to traditional *P* values.

Results

We found EPO in 38% of nests (for more details on EPO in the Lundy population, see Hsu et al. (2014, 2015).

Incubation

Most incubation observations ($N = 863$) were collected between days 9 and 12 after the first egg was laid; some were collected earlier or later (before day 9: $N = 197$; after day 14: $N = 95$). We scored incubation behavior for 186 different male sparrows at 652 broods; for 161 of those males, we have repeated observations for a total of 634 broods. In the incubation data set, there was variation in EPP within and among males (among-male variance in an intercept-only model: 1.03 [95% CI = 0.47–1.61]; within-male variance: 1.32 [95% CI = 0.74–1.92]). In the incubation data set, the link-scale repeatability of being cuckolded for males overall was $R_L = 18\%$ (95% CI = 9%–27%). There was variation in the presence EPP in a brood within and among pairs (among pairs: 1.44 [95% CI = 0.69–2.13]), and the link-

scale repeatability was $R_L = 26\%$ (95% CI = 15%–35%). This data set contained information on 194 females. There was also variation in infidelity (the presence of EPP in the brood) within and among females (among-female variance: 1.05 [95% CI = 0.49–1.69]; within-female variance: 1.39 [95% CI = 0.77–2.01]), and the link-scale repeatability was $R_L = 17\%$ (95% CI = 10%–27%). Male incubation decreased slightly with clutch size (table 1). Male incubation time was not associated with the number of EPO in the brood (table 1); we did not therefore proceed further with the analyses on male incubation time.

Nestling Provisioning

Observations of nest box visits ($N = 1,430$) were mostly collected on days 7 ($N = 564$) and 11 ($N = 496$) after the chicks hatched. However, the full data set of observations used in this analysis spans the entire nestling period. The data set on nestling provisioning comprised observations of parental care by 207 male sparrows, caring for 661 different broods. Two hundred males (97%) were observed more than once. We had five or more observations for 121 individual males (50%). Of all males, 76% were observed at more than one brood and 53% were observed at three or more broods; 57% (118) were observed at multiple broods with variation in the number of EPO. There was variation in the degree of cuckoldry experienced both within and among males (among-male variance in an intercept-only model: 1.09 [95% CI = 0.45–1.69]; within-male variance: 1.38 [95% CI = 0.78–1.97]). The link-scale repeatability of EPP for males was $R_L = 19\%$ (95% CI = 9%–27%). We also assessed the variation in EPP between unique parent-pair

combinations. Of all 313 unique pairs, 126 pairs (40%, including 37% of males, or 77 individuals) had at least two broods that varied in the number of EPO. There was variation in the presence of EPO in a brood among (1.41 [95% CI = 0.67–2.17]) and within (1.11 [95% CI = 0.45–1.76]) pairs. The link-scale repeatability of the presence of EPO among pairs was $R_L = 24\%$ (95% CI = 13%–34%). There were 204 unique females in the data set and variation in the number of offspring resulting from EPP within and among females (among-female variance in an intercept-only model: 2.34 [95% CI = 1.62–3.18]; within-female variance: 0.63 [95% CI = 0.37–0.88]). The link-scale repeatability of EPP among females was $R_L = 38\%$ (95% CI = 29%–45%).

Within-Male Adjustment versus Between-Male Effect. We found within-male adjustment: individual males visited nests with a lower frequency when there were more extrapair offspring in their brood (table 1). Back-transforming the estimate revealed that with an increase of 1 SD in EPO in the nest (which corresponds roughly to one EPO offspring in a brood of four), males reduced their paternal care by 1.15 times the standard deviation in paternal care. The parameter estimate for the between-male effect was not statistically significant but was similar in direction. The difference between the between- and within-male slopes was not statistically significant because the 95% CIs overlapped.

Effect of the Partner. We found that individual males significantly adjusted their paternal care between pairs ($W_m B_p$) by a magnitude similar to that reported above (back-transformed: 1.15 SD). The point estimates for the parameters within males within pairs—as well as for between males—were

Table 1: Generalized linear mixed models of male house sparrow parental care

	Incubation time (min h^{-1})			Nestling visits (h^{-1})		
		95% CI			95% CI	
	b	Lower	Upper	*b*	Lower	Upper
Fixed:						
Intercept	**.25**	**.23**	**.27**	**2.06**	**1.90**	**2.23**
W_m	.01	−.01	.03	**−.06**	**−.10**	**−.02**
B_m	.00	−.02	.02	−.03	−.08	.02
Chick age	NA	NA	NA	**.06**	**.03**	**.10**
Clutch size	**−.02**	**−.03**	**−.01**	**.18**	**.13**	**.23**
Day	NA	NA	NA	**.06**	**.02**	**.11**
Random:						
Male ID	.00	.00	.00	.06	.02	.09
Brood ID	.00	.00	.01	.18	.13	.22
Year	.01	.00	.01	.05	.01	.13
Residual	.03	.02	.03	.12	.09	.14

Note: Gaussian model for incubation time, and Poisson model for chick provisioning. W_m and B_m refer to the within- and between-male effects of being cuckolded. All predictors were scaled, so parameter estimates (*b*) are standard deviations. CI, credibility interval; ID, identification; NA, not applicable. Values in bold indicate statistical significance.

negative, but the 95% CI did span 0 (W_{mp} and B_m; fig. 2). The 95% CIs of these estimates overlapped.

Male State. We detected a statistically significant interaction of the within-male adjustment (W_mB_p) with the number of EPO a male gained with other females (fig. 3). Thus, a male's loss of paternity to cuckoldry and his gains from EPP had more than additive negative effects on paternal care. For each standard deviation by which males gained EPP (roughly one chick), they reduced their paternal care by 1 SD. We found that the 95% CIs of the interactions of the adjustment with the age of the male or its squared age all overlapped 0; thus, we removed these terms from the final model presented in figure 3.

Environmental Effects. We found that males did not adjust paternal care relative to any of the environmental covariates. Specifically, neither the main effect nor the interaction of whether a brood received unrelated foster offspring (fostered) with W_mB_p was statistically significant; thus, we removed these environmental covariates from the final model. The 95% CI of the interaction of W_mB_p with brood order and the interaction of W_mB_p with day both overlapped with 0 and so were also removed from the final model.

Finally, we detected considerable negative covariation between the probability of the male being cuckolded and the age of a male but no significant effects between males

of different ages (GLMM with being cuckolded as the response variable, effects of within- and between-male age as covariates, and male ID as a random effect; parameter estimates b and 95% CI of a Poisson GLMM, responses scaled: $b_{intercept}$: −0.76 [−0.92 to −0.61]; $b_{between\text{-}male\ age}$: 0.12 [−0.03 to 0.28]; $b_{within\text{-}male\ age}$: −0.07 [−0.12 to −0.04]; $\sigma_{male\ ID}$: 1.07 [0.77 to 1.33]; $\sigma_{residual}$: 0.004 [0.00 to 0.006]). The difference between the between- and within-male age effects was statistically significant, since their 95% CIs did not overlap. Thus, with each standard deviation of increasing age (1.4 years), individual males had roughly 1.6 fewer cuckolded chicks to care for.

Discussion

We have used an exceptionally extensive data set with many repeated observations to improve our understanding of the consequences of female infidelity on male paternal care. We found no evidence for a between-male effect. However, we found support for within-male adjustment of parental care to extrapair paternity in the brood. Individual male house sparrows changed the frequency with which they paid feeding visits to the nest when their female partner subjected them to different degrees of cuckoldry. Females showed moderate to high repeatability in the proportion of offspring in their brood that were sired by extrapair males. Therefore, most within-male adjustment of paternal care occurred when the
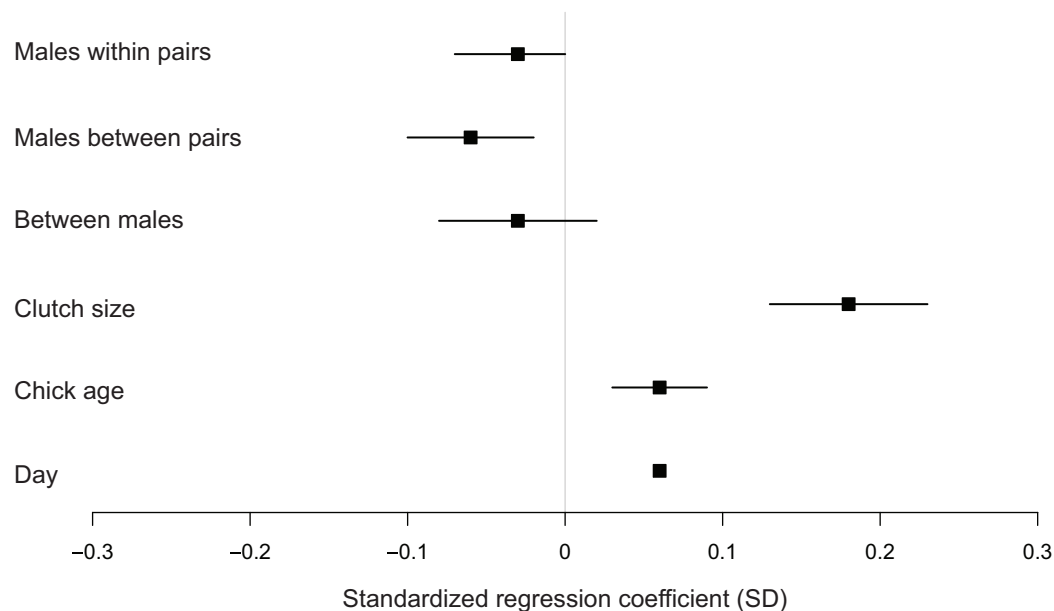
Figure 2: Regression coefficients of the variables affecting male house sparrow parental care (from a Poisson generalized linear mixed model; chick provisioning in nest visits h⁻¹). Males within pair (W_{mp}), males between pairs (W_mB_p), and between-male (B_m) effects. Predictors were scaled. Random effects that we included in the model (posterior means and 95% credibility intervals) were male identification (ID; 0.03 [0.01–0.08]), pair ID (0.03 [0.00–0.09]), brood ID (0.17 [0.12–0.22]), year (0.05 [0.01–0.13]), and the residual variance (0.12 [0.09–0.14]).
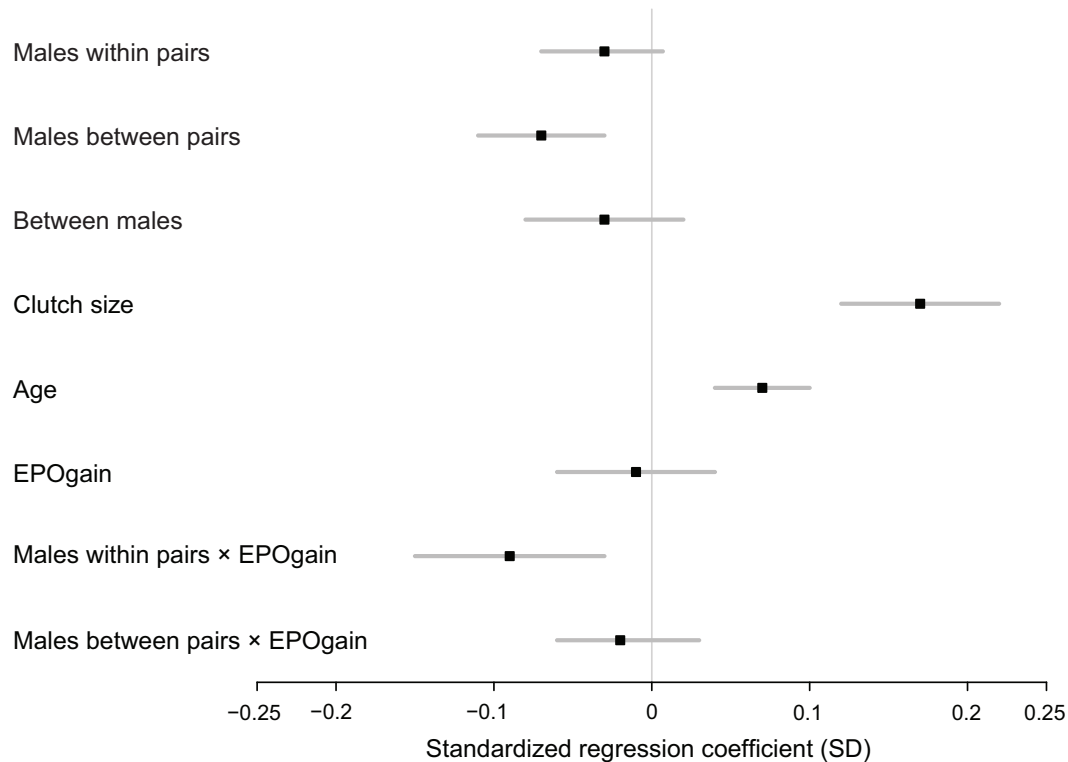
Figure 3: Regression coefficients of the variables affecting male house sparrow parental care (from a Poisson generalized linear mixed model; chick provisioning in nest visits h^{-1}). Males within pair (W_{mp}), males between pairs ($W_m B_p$), and between-male (B_m) effects; age of the male (age) and the number of extrapair offspring (EPO) the male gained with other females in that year (EPO gain); and interactions. Predictors were scaled. Random effects included in the model (posterior means and 95% credibility intervals) were male identification (ID; 0.05 [0.02–0.09]), pair ID (0.001 [0.00–0.004]), brood ID (0.17 [0.13–0.23]), year (0.04 [0.03–0.11]), and the residual variance (0.11 [0.09–0.14]).

males changed mates. There was no change of within-male adjustment when the brood received unrelated foster offspring or not. Therefore, male sparrows do not use a direct cue about their relatedness to the offspring in the brood to decide how much care to deliver. However, note that this is not a comprehensive test for whether males can discern kinship because they might use a different cue to adjust paternal care (Kempenaers and Sheldon 1996). We did not find between-male effects or within-male adjustment for incubation behavior, perhaps because incubation activities invoke different constraints than provisioning behavior. For instance, there may be sex differences in how the workload is shared between the pair members. Other reasons might be that there are severe consequences to eggs if they are not attended regularly or that incubating eggs might not be as costly as provisioning young, so that the cost of adjusting this effort might not be worth the benefit.

Our findings suggest that the majority of within-male paternal care adjustment was in response to the identity of the individual female with which a male was paired. This may reflect a within-male adjustment to differences in fe-

male quality (Alonzo 2010; Wilson and Nussey 2010). This suggestion is important because it challenges the general assumption that males dynamically optimize their reproductive investment for a given brood, using strict economical calculations based on the brood's value. Here, the brood's value may be less defined by its relatedness to the male and more by the individual traits of the female. Males might use female identity—or an unknown cue that is linked to her identity—to make decisions about their parental investment (Houston et al. 2005). Our results support the idea that birds with biparental care, such as the house sparrow, use a sealed-bid model, at least within a pair, to determine how much to invest into a brood (Schwagmeyer et al. 2002). It is possible that sparrows adjust to changes in the extrapair rate when staying with the same partner but that we could not detect such an effect; this could be partly due to females showing relatively consistent extrapair behavior. A sealed bid cannot be precisely optimized and will inevitably lead to variation in paternal care. The level of the sealed bid is not often specified and is generally assumed to happen within a pair—that the bid stays sealed as long as a pair

stays together—but not between pairs; our results support this assumption.

Our results suggest that females vary consistently in their infidelity, and it is possible that this is associated with variation in other female traits (Forstmeier et al. 2014). We do not know what cues males use to assess female identity and adjust paternal care accordingly. If female infidelity is advertised, or correlated with an unknown cue, males could use that to adjust their behavior. Our results warrant more research into these interacting effects between female and male behavior in a pair. Such interacting within-male effects between mating partners are likely to be frequent and have the power to challenge our traditional models about sexual conflict, mate choice, and parental care (Westneat and Stewart 2003; Alonzo 2010; Lehtonen and Kokko 2015) but have not often been investigated (Alonzo and Heckman 2009).

The costs of caring for unrelated young are obvious. For instance, in house sparrows, any risk of reduced paternal care is costly because males who care less raise fewer recruits annually and over a lifetime (Schroeder et al. 2013). However, the possible benefit to males of raising unrelated young may be more difficult to assess and is therefore not often considered. Aspects of a female's quality may be correlated with her propensity to obtain extrapair matings and produce EPO (e.g., Rosivall et al. 2009). In this case, females of high quality who also have high levels of EPO might provide direct or genetic benefits that outweigh the cost to the male of being cuckolded. In this scenario, paternal care could serve as a signal of a male's quality and be the object of female choice. Furthermore, since the costs of remating could be high (M. J. P. Simons, I. Winney, Y.-H. Hsu, J. Schroeder, S. Nakagawa, and T. Burke, unpublished manuscript), it may be beneficial for a male to care for unrelated young rather than risk losing a high-quality mate (Schwagmeyer et al. 2012). We also found that the within-male paternal care adjustment to brood EPO levels was associated with how many EPO a male himself sired. This pattern suggests that time or other resource constraints may govern extrapair behavior, and extrapair activities, in turn, may limit how much care a male can give to his social brood (Schwagmeyer et al. 2012).

The traditional models that aim to explain why females engage in extrapair behavior have recently been questioned (Forstmeier et al. 2014; Hsu et al. 2014; Nakagawa et al. 2015), because empirical data do not support the idea that females choose a higher-quality extrapair mate to make up for deficiencies in her social mate—whether to gain good genes, better matching genes, or indirect benefits—all between male effects (Arnqvist and Kirkpatrick 2005; Hsu et al. 2014, 2015). New theory is based on the finding that extrapair males are mostly older males (Cleasby and Nakagawa 2012; Hsu et al. 2015). Thus, male age is associated

with EPP, through a mechanism whereby a male's ability to gain paternity improves with age or where monogamous males selectively die younger. Male age could be associated with within-male changes in behavior that lead to improved mating success through coercion, through an improved ability to convince females, or through postcopulatory sperm competition. The latter—albeit speculative—idea is supported by our finding that males lose fewer paternities to extrapair sires as they age and also predicts that older males in general gain more paternities—extra- and within-pair—which previously has indeed often been observed (Cleasby and Nakagawa 2012). The idea that old males gain more EPP through behavioral or physiological changes with age has been coined the sugar-free daddy hypothesis—old males gaining extrapair matings but not contributing any benefits to their female (Nakagawa et al. 2015). One major differences between the so-called adaptive (good genes, genetic matching, indirect benefits) and the nonadaptive (sugar-free daddy) hypotheses is that the latter considers changes within individual males, while the former considers differences between males. This highlights the value and need of studies distinguishing within-individual male effects from between-male effects through repeated observations of individuals.

Our results prompt the question of whether a female's EPO strategy is fixed within pairs and between social mating partners. However, the costs and benefits of such a female extrapair mating strategy clearly need to be revisited, because it would incur costs to the female not only in terms of the fitness of the offspring (Hsu et al. 2014; Schroeder et al. 2015) but also in terms of reduced parental care by her social mate (this study).

In conclusion, the within-male adjustment of paternal care does not appear to be a dynamic response to the number of extrapair offspring in the brood but, rather, a response to mate quality in a sealed-bid manner within pairings. We find no evidence for a between-male effect. Our findings update the assessment of the costs of female extrapair behavior in terms of paternal care. This assessment is needed to estimate the costs and benefits of female infidelity—basic requirements for understanding the evolution of mating systems, monogamy, and parental care.

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