The costs of extra-pair mating

Jørgen S. Søraker *[1,2], Jamie Dunning[3]

[1] Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology Høgskoleringen 5, NO-7491 Trondheim, Norway

[2] Edward Grey Institute, Department of Biology, University of Oxford, Oxford, UK.

[3]Department of Life Sciences, Silwood Park, Imperial College London, UK

*Corresponding author: jorgensoraker@gmail.com

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Abstract

Extra-pair behaviours, where individuals copulate outside of an established pair bond, resulting in extra-pair paternity (EPP) of offspring, have long intrigued behavioural ecologists. Of particular interest is why females of otherwise socially monogamous species engage in extra-pair behaviours. Although researchers recognise that the drivers of variation in EPP, both within-species and between-species, also depend on the negative consequences (costs) of the behaviour to the individual, empirical studies mostly focus on benefits rather than costs. This is partly because benefits are often measured in currency close to fitness, whereas costs often have more indirect and complex pathways to fitness. Both the prevalence and magnitude of a cost are experienced in the context of the environment of the individual and may affect fitness, either directly (by affecting reproduction or survival) or indirectly (through the fitness of offspring). Here, we review our current understanding of costs associated with EPP and extra-pair copulations (EPC), e.g. both the costs of producing extra-pair offspring and the behaviour associated with EPP. We conclude that the costs of EPP and EPC are likely a key factor shaping this behaviour. More research, particularly empirical and experimental studies in taxa other than birds, is needed to understand the intricate cost-benefit equation underlying EPP.

1. BACKGROUND

Introduction

Multiple paternity is reproduction with multiple males within the same clutch. The extent of multiple paternity varies between mating systems and is particularly common in polygamous mating systems [1]. However, multiple paternity also occurs in species with mating systems regarded as socially monogamous, mainly through extra-pair paternity (EPP). EPP is any reproduction outside an established social pair – that is, offspring sired by a male other than social father. EPP is a result of extra-pair copulations (EPC), that is, copulation with partners outside the social pair. The combination of EPP and EPC, hereafter referred to as extra-pair mating (EPM), therefore covers both reproduction and the behaviour associated with it. EPP is well studied in birds [2–5], and 75% of sampled bird species regarded as socially monogamous engage in extra-pair behaviour to some extent [2]. Further, EPP is also recorded in socially monogamous species in other taxonomic groups, like mammals [6,7], reptiles [8] and fish [9].

Through EPP, males can increase the number of offspring produced without investing in costly parental care. However, the motivation for females to engage in EPC, potentially resulting in EPP, is less clear. Trivers [10] suggested that, because females are limited by the number of eggs they can lay over their lifetime, females should only seek extra-pair copulations (EPC) from males of higher quality than their social partner, increasing the quality of her offspring, and her reproductive success. However, empirical evidence for such indirect benefits to females is scarce [11–14].

Several, often conflicting, hypotheses have been proposed to explain female engagement in EPM, often focusing on the benefits for the female [2,4,15]. These hypotheses are broadly divided into direct and indirect benefits, of which both could result in EPM as an adaptive reproductive strategy for females. Direct benefits of EPM for females would increase their reproductive success or survival. For example, extra-pair males may provide insurance against social male infertility [16–18]. Other direct benefits may include access to resources [19,20], avoidance of genetic incompatibility [21,22] and increased parental care or nest defence [23,24]. Although any of these interactions may provide a benefit to individual fitness, they are unlikely to explain considerable variation in extra-pair paternity, as many studies find no evidence for such indirect benefits [24–26].

Indirect benefits increase the female's reproductive success by enhancing the fitness of her offspring. For example, a female may increase the genetic quality of her offspring by reproducing with a male of high genetic quality [11,15,27,28] or compatible with her own genes (i.e. through inbreeding avoidance; [21]). Despite these hypotheses, suggested to explain the persistence of extra-pair behaviour in females, EPP has seldom been demonstrated to provide indirect benefits in the wild [12,29].

Moreover, there are empirical examples of costs to females [30,31] or to extra-pair offspring [29,32,33]. More recent sexual conflict hypotheses therefore consider how, under certain conditions, EPM may persist while maladaptive for females. This could happen if i) EPP is an adaptive behaviour for males – the intersexual pleiotropy hypothesis [34,35] or ii) genes for other traits under positive selection also code for EPM behaviour- the intrasexual pleiotropy hypothesis [36].

The costs of EPM are central to these hypotheses because they focus attention on the disadvantage(s) for the female relative to the benefits experienced by the male [33]. Sexual conflict hypotheses have been difficult to test empirically, in part due to incomplete assessment of costs [37,38], and have mostly been supported by indirect evidence [39,40]. Thus, although sexual conflict hypotheses demonstrate that EPP could be maintained despite being maladaptive to females, measuring the relative costs is key to empirical evaluation.

Although several costs of EPM have been described (listed in Table 1), they’re scarcely studied experimentally [41–43] and difficult to demonstrate empirically without large sample sizes and precise fitness data [13]. Empirical studies, therefore, focus on identifying the reproductive benefits of EPP, but they rarely access (or are aware of) the costs in the same context. Although this is likely due to currency of benefits is easier to measure than the currency of costs, studies often also fail to consider them. For example, although obtaining EPP can increase the number of offspring for the males [44], seeking EPC also comes with search costs [41] and leaves the female unguarded in the same period, hence risking loss of within-pair paternity [45,46]. Another issue is the predominant bias toward avian studies compared to other taxa, like reptiles, mammals, fish and insects. Therefore, a biased, under-representation or underestimation of the costs may bias our understanding of EPM behaviour.

Costs of EPM can take different pathways. First, the costs of EPM can be direct [42] or indirect [33]. A direct cost reduces an individual’s fitness through reduced reproduction or survival. In contrast, indirect costs affect the fitness of offspring, for example through lowered genetic quality [23,33,40]. Direct and indirect costs are not mutually exclusive, as certain mechanisms can affect both parental reproduction/survival and offspring future fitness at the same time (e.g. reduced parental care from social partners). Second, costs can have an evolutionary or an ecological origin. An environmental (or behavioural) cost of EPM result from an individual’s engagement in EPP, whereas an evolutionary cost result from the consequences of EPP in previous generations, reflecting past selection events. One could argue that evolutionary costs are simply the result of beneficial behaviour maximizing fitness instead of direct costs to the individual [47]. Therefore, evolutionary versus environmental costs cannot always be separated. However, clarifying the origin can often avoid potential misconceptions.

Here, we review the negative consequences of EPM for individuals, while placing them into costs of EPC and EPP. We make the case for studying the drivers of EPM in the context of costs and benefits. In doing so, we hope this will improve our understanding of the long-standing question of extra-pair paternity, particularly from the female perspective.

The costs of extra-pair paternity

In this section, we review identified costs (Table 1) associated with extra-pair paternity under nine headings, each representing a cost: 1) reduced paternity, 2) costs of acquiring extra-pair mates, 3) mate guarding (and its effect on paternity), 4) reduced genetic quality as a result of EPP, 5) transmission of sexually transmitted disease, 6) offspring competition, 7) harassment, 8) divorce rates, and, 9) reduced parental care.

1) Reduced paternity

From an individual's perspective, loss of within-pair paternity (through female EPP) is the most apparent, and likely highest cost of EPP for males [2]. Loss of paternity is a direct cost of EPP, as it reduce the number of offspring produced [5]. Although studies have investigated the fitness benefits of obtaining EPP [44], fewer have investigated the reduced fitness due to loss of paternity (i.e. the reduced lifetime reproductive success), a consequence that deserve closer investigation. From studying characteristics of males obtaining EPP, we know that reduced paternity is dependent on both quality and age of the male. For example, male of bird species often obtain more EPP with age [48], although the evidence for an effect of age on within-par paternity is mixed [44,49].

Although focusing on the costs of EPP for the individual, one should note that reduced paternity could also be a population-level cost of EPP as it can affect both adaptation and population dynamics. For example, EPP can influence variance in reproductive success [44], thereby affecting the effective population size [50]. In song sparrows, *Melospiza melodia*, O'Connor et al. [51] showed that EPP had a low effect on effective population size by comparing estimates of effective population size from social and genetic data. Another way to investigate how EPP influence effective population size is to decompose the demographic variance to understand its sensitivity to variation in reproductive success, but such empirical studies in birds are lacking [52]. Increased variance in reproductive success caused by sexual selection may also affect the evolvability of a species due to reduced genetic variation, commonly referred to as the 'lek paradox' [53–55]. However, the potential role off EPP in this paradox through affecting sexual selection remains poorly understood.

2) *Costs of acquiring extra-pair mates*

The costs of acquiring an extra-pair mate have traditionally been split into search cost [41], and the energetic costly display for extra-pair partners [56]. However, they have received little empirical attention, particularly experimentally [41]. All these costs have been proposed under a system of adaptive EPP [15,41], and are experienced by either sex, affecting the same individual (i.e. the individual seeking EPC).

Search costs (i.e., the cost of physically searching for an extra-pair partner) can be viewed as a time cost, lost opportunity cost and/or an energetic cost. The travel distances required to find potential extra-pair partners can be extensive [57,58] but the energetic expenditure is expected to be low [41]. Indeed, extra-pair partners are often neighbours [24,59–61]. Experimental evidence suggests that search cost may affect the distribution, but not the level, of EPP. Dunn & Whittingham [41] experimentally increased search costs by cutting wing-feathers of female tree swallows *Tachycineta bicolor*, and found similar EPP rates for wing-cut versus control females, but wing-cut females had more local extra-pair partners. Search costs may also be the reason why several studies find population density to be a determinant of EPP rates [5] because higher densities could reduce search costs.

While searching for an extra-pair partner, time spent away from the nest also increases the risk of others stealing nest material [62]. Although this is an untested hypothesis, stealing of nest material has been reported in multiple bird species [63,64], and maybe a relevant cost of EPM worth further investigation. Further, this time away from the nest also makes it prone to brood parasitism [65]. However, no study link risk of brood parasitism to EPM behaviour through this mechanism specifically.

When an extra-pair partner is located, courtship displays towards this potential partner may be required [56]. Courtship displays are expected to have time and energetic costs, although these might be relatively small direct costs [66]. Experimental studies would again be useful for properly assessing display costs of EPP, because they could control for potential confounding effects, such as individual quality and state. Although challenging, such experiments could manipulate the need for display (through skewed sex ratio, physically separating the sexes etc.) and track fitness either through reproduction or state (e.g. through relative body mass).

3) Mate-guarding

Mate-guarding, where the male follows the female to avoid her engaging in EPC, occurs often in the wild [15,67,68]. Mate guarding potentially results in physical conflict with other males [69], thus resulting in both energetic costs [43,70] and time (lost opportunity) costs [42] for the guarding male.

To study the energetic cost of mate-guarding in Seychelles warblers *Acrocephalus sechellensis*, Komdeur [42] experimentally manipulated the density of neighbouring males, hence changing the necessity of mate-guarding. This study demonstrated a negative relationship between relative body mass (i.e., energetic state) and time spent mate-guarding. Moreover, the experimentally induced reductions in mate-guarding resulted in substantial increases in male relative body mass and time spent foraging. Mate-guarding was also demonstrated as energetically costly for other birds [43], mammals [68] and spiders [71]. Reduced energy intake during mate guarding is also documented in reptiles [70]. Therefore, mate-guarding can be a direct cost for males, as reductions in male body mass are expected to be associated with reduced survival [72].

Although the extent of mate guarding varies [15,43], high-quality individuals have been shown to perform less guarding [67]. This may be because females prioritize mating based upon the social males relative ‘quality’ [67]. A decrease in guarding with individual quality is also predicted by theoretical models [73]. Hence, high-quality individuals are likely to exhibit a lower cost of paternity assurance. However, measures of male ‘quality’ are often attributed to individual quality markers such as body size or sexually-selected signals [67]. This represents an among-individual quality effect, but few studies have focused on the within-individual quality effect of energetic state (i.e., relative body mass or fat reserves) which would be interesting to understand within- versus between individual cost-variation.

The costs of mate-guarding can be reduced by guarding only during the partner’s fertile period [58,74,75]. In several species, males guard their social partner throughout their fertile period and seek extra-pair mating outside this period [58,75]. Furthermore, the costs of mate-guarding could be lowered by reducing the intensity of guarding behaviour. However, intensity of chasing potential conflicting males was independent of relative body mass in guarding male Seychelles warblers [42]. This indicate that energetic state may affect only the extent of mate-guarding, rather than the intensity of the behaviour itself [42]. Interestingly, mate-guarding could also have the by-product benefit of increasing the partner’s condition, because the presence of an alert partner could reduce the female’s adaptive level of anti-predator vigilance, which could enhance an indirect benefit of mate-guarding [76].

Although direct costs of mate-guarding have been demonstrated, no studies have explored potential indirect costs of mate-guarding. If mate-guarding reduces the energetic state of males in species with obligate biparental care, this might reduce potential for male care, with potential effects on offspring quality.

4) *Reduced genetic quality*

Increased genetic quality for offspring by higher quality genes from extra-pair males is one of the main hypotheses regarding EPP [11,12]. However, when mating with extra-pair partners, females also risks reducing the genetic quality of the offspring [13]. Females indirectly assess the genetic quality of extra-pair mates, for example via secondary sexual traits [4,77]. These traits might, or might not, be reliable indicators of male quality, potentially reducing the female’s ability to sample the quality of potential mates sufficiently [56]. Uncertainty in accessed male quality can therefore result in sub-optimal genetic assessment both of the social and the extra-pair partner [78]. Thus, females impose, either intended or non-intended, the cost to the offspring. Sperm choice, where the female choose between sperm from several mated males is thought to partly solve this problem (e.g. choosing only social males sperm), but there is only limited evidence in some species for differential male sperm selection by females [15].

Analysis regarding the genetic quality of offspring needs to be rooted in one or more fitness components. A variety of fitness components have been used, but one should be careful in the choice when multiple components are available, as they potentially answer different questions. If multiple fitness components are measured, multivariate analysis now allows for useful interpretation of the covariance-matrix, allowing the use of multiple fitness components [79]. Studies have stated that lifetime reproductive success may be the optimal fitness estimate [33,40], but often cost and benefits are only apparent in the short-term [80]. However, cases may arise where it is natural to look to other fitness components, particularly if one has detailed knowledge of fitness measurements in the population [80], and *a priori* hypothesis are made about certain fitness relationships.

Most studies find no difference between extra-pair offspring (EPO) and within-pair offspring (WPO) in measurable fitness components [12], and few studies find EPO have lower fitness than WPO [40]. Sardell et al. [40] used song sparrows *Melospiza melodia* to study survival, recruitment and lifespan and how they differed between EPO and WPO. They demonstrated a sex-specific genetic cost regarding EPO, with female EPO having lower recruitment and shorter lifespan than WPO females. However, this was not demonstrated in male offspring, underpinning the important aspect of sex-dependency while comparing EPO and WPO.

When studying American crows *Corvus brachyrhynchos*, Townsend et al. [23] found that EPO were more inbred than WPO. Inbreeding is found to lower survival in this population [81], resulting in an indirect cost of EPP. Again, it can be useful to consider population-level costs of EPP. Population-level costs can be lowered effective population size, reduced evolvability, reduced genetic variation (See reduced paternity) and population-level inbreeding depression, with potential severe consequences also at population level [82].

Thus, it is likely a restricted cost of EPP. Indeed, none of the examples have shown an effect on the reproductive fitness of offspring, likely caused by lack of power. However, this is expected if reduced offspring genetic quality is a large cost of EPP, and not all poor-quality offspring die prior to recruiting into the breeding population.

5) Sexually transmitted diseases (STDs)

Pathogens can affect individual fitness, population dynamics [83,84] and sexual selection [85]. As several pathogens can be transmitted during mating, promiscuous behaviour has been suggested to increase the prevalence of sexually transmitted diseases (STDs) in both individuals and species [86]. Sheldon [87] defined an STD as "… any pathogen that is transmitted during the act of copulation", a definition we follow. STDs include both pathogens transmitted via the reproductive organs [88] and ectoparasites transmitted through physical contact, such as feather parasites in birds [89–91].

STDs have been identified in multiple wild populations of birds [88,92–94], mammals [95], reptiles [95] and insects [96]. However, the ecological factors determining between-species variation in the presence and prevalence of these pathogens are still unclear, although it likely depends on for example the social environment [97]. One important factor is the effect of species-dependent life-history traits, because the presence of STDs will reflect the co-evolutionary relationship between parasite and host [98]. Therefore, it is here helpful to separate between evolutionary versus environmental costs.

Between species, a positive covariation between average EPP-rate and the presence and prevalence of STDs is expected. Such an effect would demonstrates an evolutionary cost of EPP, due to potential co-evolutionary effects between parasites and hosts [98]. In a comparison of 4 bird species with contrasting mating systems, STDs were more prevalent in more promiscuous species [92]. However, similar studies with larger sample sizes are needed to further confirm this hypothesis.

STDs are also predicted to affect individual EPC behaviour [99] as they can have a negative effect on individual fitness, imposing a direct environmental cost [87]. An increasing number of sexual partners per individual is predicted to result in higher prevalence of STDs per individual [92]. It remains unknown, however, if pathogens can potentially be transferred over to the offspring during embryo/egg development and create an additional indirect environmental cost through reduced offspring fitness. One problem when studying environmental costs of EPC is the striking variation in types of pathogens identified. Westneat & Rambo [93] studied the environmental costs of EPP in red-winged blackbirds *Agelaius phoeniceus* based on exposure to STDs, and found no effect of STDs on male fertility or female reproduction, but highlighted the need for a larger sample size. Furthermore, they demonstrated high variation in identified pathogens among males, underpinning the importance of pathogen-specific *a priori* hypothesis regarding the role of STDs. Another study found heterogeneity in pathogenic microbes among tree swallows, but this did not affect semen characteristics in the studied population [88].

If STDs reduce fitness, defence mechanisms may evolve. For example, the uropygial gland in birds produces anti-parasitic substances [90,100]. A comparative analysis of 60 bird species showed larger uropygial glands in species with higher levels of EPP, perhaps as a antiparasitic defence mechanism against the evolutionary costs of EPP [101]. Moreover, bird species with higher levels of EPP tend to have larger spleens, which are an important part of the immune system [102]. However, no within-species investigations exist linking the uropygial gland or the spleen to EPP rates, which would be of highest interest regarding among-individual variation in STDs and the evolution of defences against STD. Such co-evolutionary responses may explain low effects of EPP rates on STDs among species, because the selection for defence mechanisms may already have occurred for many of these species [98].

Recently, substantial research has focused on microbiomes- the symbiotic microbial communities in organisms. Microbiomes include pathogenic microbes, and methods for detection such pathogens have improved over later years [103]. In the rufous-collared sparrow (*Zonotrichia capensis*), the cloacal microbiome changed during the breeding season for males, and were more diverse early in the breeding season, potentially because of sexual transmission during mating [104]. However, few have tested how microbiomes relates to EPP directly, and certainly warrants further investigation [103,104]. Although caution must be used regarding the source sample (e.g. faecal sample, semen sample etc.), this technique can set the new standard for future empirical research of STDs as costs of EPC, and is particularly useful for investigating the environmental costs of EPC.

6) *Increased sibling competition*

Increased sib-sib competition provides a rarely mentioned cost of EPP [13]. It follows from theories of parent-offspring conflict, sibling competition and the effects of reduced within-family relatedness [105,106]. Such a cost is imposed either by the female (if she participate in EPP voluntarily) or by the extra pair male (through enforced copulation) while affecting the offspring and potentially both sexes.

Across species, begging loudness was found to increase with the species EPP rate [107]. This intensified begging could result in increased parental care [108], and could therefore represent a direct cost for the parent(s) that provide more than their optimum level of care. It could potentially also increase the predation risk. Environmental costs of increased sib-sib competition through begging would consider changes in begging (intensity) to variation in within-clutch relatedness, but although intensively studied, this has rarely been demonstrated [108], (but see [109] for exception). One reason why siblings do not adjust begging to sib-sib relatedness is the lack of stable paternity markers. Extra-pair mates would be selected to avoid paternity markers, which could reveal their identity for the social mate. However, weather paternity markers evolve, either genetically or through behaviour, is debated and topic for considerable theoretical modelling [110,111].

Changes in the relatedness between parents and offspring affects the parent-offspring ‘zone of conflict’ [105]. The optimal level of investment from the parent is stable or decreasing with lowered average relatedness to the offspring [112]. Simultaneously, lowered relatedness between the offspring, and between the offspring and the parent, makes the optimal level of investment for the specific offspring to increase [105]. Therefore, the amount of parental investment offspring want to extract from their parents increases [105]. In the least killifish *Heterandria formosa*, polyandrous populations with reduced sibling relatedness have stronger maternal resource extraction than monogamous populations [113], illustrating a direct cost for the female.

7) Harassment

When engaging in EPC, females may experience physical harassment from the social partner or extra-pair mates. This can be a severe direct cost of EPC and could affect the timing and occurrence for EPC [114]. However, the quantification of such harassment has so far received limited empirical attention [114]. Social males can harass their females, as deterrent 'punishment' for engaging in EPCs. This was documented in lesser grey shrikes *Lanius minor*, where females performing EPCs experienced aggression from social mates. Moreover, the study found that this harassment was not so costly for males [114]. However, we lack demonstration of this EPC-induced harassment in most species [114], although indirect studies suggest higher mortality in females engaging in multiple paternity in insects, although most of these species was not socially monogamous [115].

Females may also experience harassment from extra-pair mates, as a coercion tactic from males to obtain EPP. This harassment can result in female injury, or even death [116]. Extreme examples of harassment are comparatively rare in birds (e.g. versus mammals) and they are mostly recorded within waterfowl and the hihi *Notiomystis cincta* [117]. EPCs can also occur as a cost-avoiding strategy by females [5]. Harassment by extra-pair males may be reduced in duration and intensity if female comply with EPCs that they might otherwise avoid participating in, known as convenience polyandry [118]. Higher levels of harassment in species with higher levels of EPP remains an untested hypothesis. Between-species investigations would be informative, if not only to understand the natural variation in EPP-related harassment.

Given that harassment is costly for females, one could argue that EPCs are not female driven. However, females may still seek EPCs with certain types of males and thus risk a certain amount of harassment from other potential extra-pair mates. To reduce the cost of harassment from social and extra-pair males, EPCs could be performed cryptically compared to within-pair copulations as demonstrated in the great grey shrike *Lanius excubitor,* where within-pair copulations were performed openly, while EPC took place in more vegetative areas [119].

8) Divorce rate

Engaging in EPP may also increase the divorce rate (i.e. the rate at which social partners are changed across reproductive events). Divorce can be a direct cost, because more experienced pairs often have higher reproductive success [120]. In long-lived species, pair formation is time-consuming and individuals may miss critical reproductive opportunities following divorce [121]. Higher divorce rates is found in species with higher EPP-rates rates [122,123], suggesting an evolutionarily-based cost. More important is the environmental cost of divorce because individuals engaging in EPCs may experience a higher probability of divorce. This has been demonstrated in black-capped chickadees *Poecile atricapillus* [124], where females involved in EPCs were more likely to switch partners between breeding events. However, there were no differences in reproductive success whether the female was involved in EPCs or not. Females also divorced for males of higher status rank, indicating that they divorced for a better option, rather than as a result of being divorced by the male due to EPP. In house sparrows *Passer domesticus*, females that switched partner more often were more likely to have EPO, although they did not have a higher proportion if EPO [125] possibly implying a non-adaptive mechanism [34,125]. Divorce could be imposed by both sexes and affect the partner, as individuals would likely seek divorce only if they had better options. Therefore, the divorcing individual would likely benefit, while the divorced sex would bear the cost. The divorcing sex would also depend on the operational sex ratio [126], individual quality and other ecological and life-history characteristics.

9) Reduced parental care

Reduced parental care caused by lowered paternity is an intensively studied cost of EPP [31,127–130], because parental care is known to be particularly costly [131]. Reduced paternal is imposed by the male while directly costly for the female [132]. Theoretical models show mixed predictions for adaptive responses in care with paternity [133]. A key component in these models is the male's ability to assess paternity [133], which is still debated in taxa like birds [110,111], but common in other taxa like fish [134]. Also, clutch-specific EPP levels can be driven by male quality. In such cases, low-quality males with low level of paternity may be left with no better option than maintaining the same level of paternal care, doing "the best of a bad job". Therefore, paternity-driven paternal care might not be expected within ecological timeframes [5]. Selection over generations can, however, result in species-level responses in an evolutionary timeframe [135].

Evolutionary cost of EPP in this context mostly consider the change in average level of care in relation to the average species-level EPP-rate [127–130]. Evolutionary adaptations regarding reduction in paternal care can therefore result in selection maximizing long-term geometric fitness [47]. However, evolutionary relationships do not provide evidence of within-individual adjustments to EPP in their social clutch.

Environmental costs of EPP evaluate adaptive responses to varying levels of paternity that happens within an individual's lifespan [31,136]. A cost of adaptive within-male adjustment to EPP will be a direct cost as it calls for compensation by the female. However, it can also be an indirect cost if the female does not fully compensate, potentially resulting in lowered offspring quality [137].

Evidence from empirical studies of both evolutionary and environmental costs of reduced paternal care are mixed [127–129,136]. The results also clearly differ between different taxa. In birds, between-species studies of evolutionary cost generally show that males decrease the level of care with reduced paternity, although it is still debated which forms of care that are reduced [127–130]. Different forms of care have different implementations [25]. While some studies find pre-hatching forms of care to be affected by paternity (including incubation, nestbuilding etc.) [30,130,138], other studies support post-hatching care to be affected by paternity (provisioning) [127,129,130]. However, studies differ in their scoring of caring behaviour, underpinning the need for a yardstick when treating parental care behaviour. In fish, clear between-species investigations are lacking, but paternal care evolve under pair-spawning, where the male has some certainty of paternity, compared to group-spawning. However, this also included species with additional mating males (e.g. like sneakers) [139].

Studies on the environmental costs of EPP show weaker consistency than evolutionary costs. Several studies have been performed linking paternity and paternal care, showing support for both a reduction in care [31,77,140–142], and no effect on care [136,143–146]. In the reed bunting *Emberiza schoeniclus*, Suter et al. [141] showed that the males reduced provisioning rate in response to decreased paternity. This reduction was further compensated by the female, indicating a direct cost of EPP for the female. However, Bouwman et al. [136] did not find any evidence for such a negative relationship between level of EPP and paternal care in the same species. Fewer examples exist from other taxa than birds, but in the bluegill sunfish *Lepomis macrochirus*, males reduce their amount of care with decreasing paternity [142]. However, in this species, potentially alongside other fish species, males use olfactory cues to access paternity [147]. A between-species investigation of within-male adjustment across several taxa found no effect of paternity on parental care [148]. However, reduction in male care were more likely if the cost of caring and risk of reduced paternity were high [148]. Several of these investigations have been experimental, and cross-fostering experiments are common, particularly within birds. Cross-fostering experiments are, however, seldom informative as few know the specific cues used by males to access paternity [149]. Cross-fostering experiments generally lack trust in null-results, as one rarely knows if there is no use of kin-recognition, or if the wrong cues are manipulated. This is potentially a source to publication bias, which can further affect meta-analysis.

Due to the mixed evidence to environmental costs of EPP on parental care, it has been hard to extract some general patterns [136]. However, most studies fail to address concerns on important confounding factors [149]. Factors like environmental variation, partner quality and an individual's state are key aspects as they are all likely to affect the optimal behaviour for the male [149]. Costs to the female of reduced paternal care may also be state-dependent, and studies linking state-dependency to cost of EPP to female fitness components would provide helpful insight [150].

Schroeder et al. [31] studied paternal incubation and provisioning in house sparrows (*Passer domesticus*), while controlling for several of the suggested confounding effects [149]. They disentangled within- versus among-male differences in care related to varying paternity. The study found that females consistently differed in their individual EPP-rate. Males reduced provisioning only when mated with a female consistently engaging in EPP. Therefore, males adjusted the within-male level of care to the female identity, rather than the paternity-level in the clutch, questioning the use of same-pair studies of paternity to care relationships [149]. A cross-fostering experiment suggested that males did not use kin-recognition to adjust provisioning. To fully understand the role of paternity on parental care, more studies accounting for confounding factors [149] are needed. Further, disentangling within- and among-male adjustments are informative to understand the potential (and confounding) effect of difference in male 'quality' and how it relates to a male's response to loss in paternity.

The study of reduced parental care as a cost of EPP therefore lacks a clear consensus from an environmental perspective. However, few have applied a statistical decomposition that clearly accounts for demonstrated confounding factors. Studies should include considerations like pair-constitution, environmental variation, individual state and whether the measured trait is a reliably proxy for parental care. Moreover, studies in other taxa than birds are highly needed.

CONCLUSIONS

Studying the costs of EPM is helpful for understanding variation in EPM rates across both individuals and species. Costs of EPM likely play a significant role in shaping EPM behaviour. However, quantifying these costs is often difficult, and therefore poorly studied, and *apriori* hypotheses are needed. Moreover, bias toward avian studies amy limit our general understanding of EPM, both in terms of benefits and costs. Studies into the consequences of EPP beyond the birds would be beneficial.

To date, however, the strongest costs seem to be reduced paternity and reduced parental care by the social partner. The cost to females is still largely misunderstood, despite many decades of research, and we suggest that an improved understanding of costs (rather than the traditional approach of defining empirical benefits) may yield new research direction.

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Tables

Table 1: Identified costs of EPP, regarding costs as direct or indirect, what sex the cost is imposed by and which individuals that bear the costs.

Cost	Type of EPM	Direct or indirect	Imposed by	Affecting	Ref.
Reduced paternity	EPP	Direct	Female?	Male	[4]
Cost acquiring partner	EPC	Both	Any sex	Same individual	[41]
Mate guarding	EPC	Direct	Male	Same individual	[42]
Reduced genetic quality	EPP	Indirect	Female	Offspring	[40]
STD	EPC	Both	Any sex	Same individual and partner	[133]
Increased sib competition	EPP	Both	Female	Offspring	[107]
Harassment	EPC	Direct	Male	Female	[151]
Divorce risk	EPP	Direct	Any sex	Partner	[122]
Reduced parental care	EPP	Both	Female	Male	[31]